

Description of Zeratulidae fam. nov. (Littorinoidea), with Comments on an Antarctic Littorinid Gastropod

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Abstract. *Zerotulidae* fam. nov. is described and placed in the Littorinoidea. The family includes the genera *Zerotula* Finlay, 1926 (formerly in Architectonicidae); *Frovina* Thiele, 1912 (synonymized with *Prolacuna* Thiele, 1913, both formerly in Naticidae); *Trilirata* Warén & Hain, gen. nov. (type species *Prolacuna trilirata* Thiele, 1912, Antarctic); and *Dickdellia* Warén & Hain, gen. nov. (type species *Laevitorina (Corneolitorina) labioflecta* Dell, 1991, Antarctic, bathyal).

The following new species are described: *Frovina angularis* Warén & Hain (New Caledonia, bathyal), *Zerotula incognita* Warén & Hain (North Atlantic, abyssal), *Z. stellapolaris* Warén & Hain (Antarctic), *Z. coronata* Warén & Hain (New Zealand, shelf), *Trilirata sexcarinata* Warén & Hain (Antarctic), *T. triregis* Warén & Hain (New Zealand, shelf), and *T. herosae* Warén & Hain (New Caledonia, bathyal). The anatomy is described for *Frovina soror* Thiele, 1912, *F. indecora* (Thiele, 1912), *Zerotula stellapolaris*, *Trilirata macmurdensis* (Hedley, 1911), *T. sexcarinata*, and *D. labioflecta*.

Antitrichotropis wandelensis (Lamy, 1906) (formerly in Capulidae, Neotaenioglossa) is transferred to Laevitorininae (Littorinidae), based on examination of radula and external morphology of the head-foot. It is classified in *Laevitorina*, subgenus *Pellilacunella*.

INTRODUCTION

The genera *Prolacuna* Thiele, 1913, *Frovina* Thiele, 1912, and *Zerotula* Finlay, 1926, have for a long time been classified in the Naticidae (*Prolacuna* and *Frovina*) and in the Architectonicidae (*Zerotula*). The only basis for this has been a misidentified naticid (*Prolacuna* and *Frovina*) and the planispiral shells of the species placed in *Zerotula*. Examination of types and additional material proved these classifications, dating from the first half of this century, to be mistakes. The genus *Zerotula* actually contained species of archaeogastropods, neotaenioglossates, and heterobranchs. When Hain obtained numerous Antarctic specimens of these groups, we decided to make a closer investigation of their systematic relationships.

We have examined the anatomies of the type species

(or, in the case of *Zerotula*, a species similar to the type species) to get a more robust basis for the systematic placement of these taxa. We have also examined, in as much detail as our material allowed, several additional species about which we had accumulated information during many years of routine examination of museum collections and expedition material.

MATERIALS AND METHODS

Our work is largely based on specimens obtained during cruises of R/V *Polarstern* in the Weddell Sea and adjacent areas between 1985 and 1991. It has been supplemented by examination of type material and specimens from other sources according to our needs. Our material is listed under each species and deposited in the following museums: AMS,

Australian Museum, Sydney; BMNH, Natural History Museum, London; MNHN, Muséum National d'Histoire Naturelle, Paris; MNZ, Museum of New Zealand, Wellington; NMWZ, National Museum of Wales, Cardiff; RSM, The Royal Scottish Museum, Edinburgh; SMNH, Swedish Museum of Natural History, Stockholm; USNM, National Museum of Natural History, Washington D.C.; ZMHU, Zoologisches Museum der Humboldt Universität, Berlin.

The material from the *Polarstern* cruises is referred to under each species by PS (*Polarstern*) followed by the cruise and station numbers. In order to avoid unnecessary repetition, we give a list of the station data below and repeat only depth and approximate longitude in the lists of "Material examined."

R/V *Polarstern* (PS) Antarctic stations

Roman numbers/Arabic numbers are cruise/leg number.

III/3, sta. 345, 73°23'S, 021°37'W, 617 m, February 1985.
VII/4, sta. 224, 71°15.8'S, 013°04.2'W-71°15.8'S, 013°01.7'W, 186-187 m, 25 January 1989.
VII/4, sta. 230, 75°14.2'S, 026°59.4'W-75°12.9'S, 027°01.2'W, 270-280 m, 30 January 1989.
VII/4, sta. 250, 74°35.1'S, 029°39.9'W-75°32.4'S, 029°53.0'W, 799-810 m, 04 February 1989.
VII/4, sta. 272, 73°26.9'S, 021°33.6'W-73°25.7'S, 021°30.2'W, 409-406 m, 13 February 1989.
VII/4, sta. 274, 71°38.8'S, 012°09.4'W-71°38.3'S, 012°13.1'W, 196-212 m, 15 February 1989.
VII/4, sta. 282, 71°31.7'S, 012°27.4'W-71°30.6'S, 012°29.3'W, 609-575 m, 18 February 1989.
VII/4, sta. 284, 71°12.0'S, 013°14.0'W-71°12.2'S, 013°16.8'W, 402-412 m, 18 February 1989.
VII/4, sta. 289, 71°12.0'S, 013°27.9'W, 672 m, 19 February 1989.
VII/4, sta. 291, 71°06.1'S, 012°33.5'W-71°05.9'S, 012°34.8'W, 499-515 m, 19 February 1989.
VII/4, sta. 293, 71°06.2'S, 012°53.8'W-71°05.7'S, 012°58.4'W, 771-793 m, 20 February 1989.
VIII/5, sta. 491, 73°69'S, 022°42'W, 390-370 m, 21 February 1990.
IX/3, sta. 165, 70°18.9'S, 03°15.8'W-70°19.2'S, 03°16.8'W, 191-204 m, 17 February 1991.
IX/3, sta. 173, 70°00.5'S, 07°09.1'E-70°00.4'S, 07°07.4'E, 739-765 m, 20 February 1991.
IX/3, sta. 174, 69°43.7'S, 10°44.7'E-69°42.4'S, 10°47.5'E, 432-432 m, 21 February 1991.
IX/3, sta. 179, 69°58.9'S, 08°00.7'E-69°59.3'S, 07°59.9'E, 185-161 m, 22 February 1991.
IX/3, sta. 180, 69°57.4'S, 06°19.0'E-69°57.7'S, 06°21.0'E, 280-298 m, 23 February 1991.
IX/3, sta. 206, 69°06.9'S, 10°01.0'E-69°46.8'S, 10°01.6'E, 343-338 m, 07 March 1991.

IX/3, sta. 207, 69°57.4'S, 05°08.4'E-69°57.5'S, 05°00.4'E, 213-210 m, 07 March 1991.

IX/3, sta. 211, 69°58.9'S, 05°08.4'E-69°57.9'S, 05°00.4'E, 661-742 m, 10 March 1991.

IX/3, sta. 212, 70°00.5'S, 03°56.4'E-70°00.4'S, 03°57.3'E, 568-644 m, 11 March 1991.

IX/3, sta. 220, 70°24.1'S, 06°07.6'E-70°24.3'S, 06°08.6'E, 118-126 m, 13 March 1991.

Further data on the work during *Polarstern* VII/4-5 can be obtained in "Berichte zur Polarforschung," vol. 68 (1990); for cruise IX/3, vol. 100 (1992); and for earlier cruises in Hain (1990).

The material from the *Polarstern* Antarctic Expedition IX/3 was processed as follows. From each trawl 50 liters of sediment that passed a 4 mm sieve were subsequently sieved on a 0.5 mm sieve. The material that remained in the sieve was saved and fixed in 95% alcohol (to compensate for water in the sediment). These residues were then sorted under a stereomicroscope at SMNH and turned out to be very rich in small mollusks (Warén & Hain, 1992).

Serial sections were prepared of a range of species, as the material allowed. The sections were cut 5-7 μ m thick and stained with Ehrlich's hematoxylin-eosin (EHE). Regrettably, all material available for this work had been preserved in alcohol (of varying strength since it was used for fixing sediment samples), which is not good for most histological purposes. The sections were therefore not of good quality, but have allowed a more precise systematic allocation than only external morphology would have done.

Egg capsules were identified to species by SEM examination of larvae ready to hatch and comparison with protoconchs of adult specimens.

We have divided the anatomical descriptions into two main parts: (1) what can be seen from the outside after removing the shell, including features seen only by transparency; (2) the results from serial sections.

SYSTEMATICS

Mollusca, Gastropoda, Neotaenioglossa

Superfamily LITTORINOIDEA

The superfamily has been discussed by Ponder (1988), Haszprunar (1988), and Reid (1989); and we refer to these papers for general information about the taxon.

Family ZEROTULIDAE Warén & Hain, fam. nov.

Diagnosis: Small to medium-sized neotaenioglossates with a featureless, planispiral to turbiniform shell with no or mainly spiral sculpture. Protoconch large, simple, and smooth, not distinctly demarcated (encapsulated development). Radula long, slender, with 80-200 transverse rows and more than 8-times as long as broad. Central tooth usually with a ridge projecting above cusps. Lateral tooth lacking "littorinid notch." Outer marginal very slender

except basally; usually with long cusps; often with weak zone and membranous cusp at mid-length. No pallial tentacle; no metapodial tentacles. Esophagus with large esophageal gland and with lateral pouches in at least some species. Penis below and to the right of right cephalic tentacle. No paraspermatozoa. Sperm often stored in pericardium of female, sometimes also in a dorsal seminal receptacle opening between albumen and capsule gland of oviduct (*Trilirata*) or in albumen gland (*Dickdellia*). Pedal ganglia with a single accessory ganglion innervating propodium or two accessory ganglia innervating pro- and mesopodium, respectively. Osphradium long, slender; a low ridge containing osphradial ganglion between two slightly taller ciliated ridges.

Remarks: Four genera are included in this new family, *Zerotula*, *Trilirata* gen. nov., *Frovina*, and *Dickdellia* gen. nov. Warén originally recognized them as probably being related from radular characters, especially by the “hooded” (Reid, 1989) central tooth and the outer marginal teeth, which have unusually long apical cusps. Furthermore, the outer marginals, and sometimes also the inner marginals, are separated from the more central teeth by a bare zone of radular membrane. The radula is 8–20 times as long as broad, and it is usually difficult to unfold the marginal teeth. It differs drastically from the much shorter and broader (3–4 times as long as broad) type present in the Rissooidea (based on Rissoidae Gray, 1847, which name was given precedence over Truncatellidae Gray, 1840; ICZN Opinion 1664).

When additional material with preserved soft parts became available during Hain’s work on Antarctic mollusks, we examined several species anatomically. This revealed similarities in the anatomy, despite the variations in shell morphology.

Systematic position of Zeratulidae: The anatomy seems highly plesiomorphic for the “rissooid-cingulopsoid-littorinoid radiation” as understood by Ponder (1988). *Dickdellia* differs considerably from the three other genera, and its special features are discussed under that generic heading.

The shells of zeratulids are about as featureless as gastropod shells come, but quite variable within the family (cf. Figures 1, 10A–C, 16, 19). None of the species so far included in the family has planktotrophic larvae, and the protoconch is thus of no use for classification. All species lack an “inner chitinous layer” (Ponder, 1988; Reid, 1989), known from Skeneopsidae, Cingulopsoidea, and some Rissooidea.

The cephalic tentacles are highly contractile and do not have any arrangement of conspicuous cilia and cirri, characteristic of most Rissooidea and Cingulopsoidea. This lack is shared with the other Littorinoidea, including the Eatiellidae. This is probably a plesiomorphy, since it is shared with most neotaenioglossates.

A posterior pedal gland is present in many groups of

the Neotaenioglossa, especially among the small species. It is, however, also common in veligers, also of large Neotaenioglossa and neogastropods (see, e.g., Fioroni, 1966), and may be a larval organ of general occurrence, retained only in certain taxa of small species, where a thin mucus thread helps prevent the adults from being washed away from the substrate. In such species, the gland usually opens via a well-defined pore centrally and ventrally on the sole of the foot. This seems not to be the case among zeratulids, where the gland is voluminous but lacks a defined opening. We therefore assume that there must be numerous, hardly discernable openings for the mucus. A posterior pedal gland is missing in adult Littorinidae (Reid, 1989).

The position of the penis, distinctly below the right cephalic tentacle, seems restricted to the Littorinidae and **Zerotulidae**. Reid (1989) considered this position apomorphic for littorinids. Now knowing this also in **Zerotulidae**, we find it more likely to be a plesiomorphy of Littorinoidea.

The innervation of the penis is of considerable interest, both for the understanding of the evolution of this organ and for the systematic position, since there seems to be variation in this between the families (see Ponder, 1988; Reid, 1989). The quality of the sections did not allow any certain conclusions since it could be seen only in *Z. stellapolaris*, and even in that species, the nerves could not be followed without interruption to their origin. It seems, however, that there are nerves both from the subesophageal and right pedal ganglia that join to a “penial ganglion,” posteriorly at the base of the penis. From this “penial ganglion,” there are also nerves to the pallial sperm duct and the prostate, and it is possible that the nerves to the penis are those from the pedal ganglion, and the ones to the sperm duct and prostate come from the subesophageal ganglion. The “penial ganglion” may then be a secondary fusion for coordination of the differently derived components of the male reproductive system (zygoneury). A similar zygoneury was described by Bouvier (1887) in *Littorina littorea*, but the relations to the penis were not mentioned.

This type of penial innervation is known from Annullariidae and Pomatiasidae, but we cannot exclude that it occurs elsewhere in the Rissooidea-Cingulopsoidea-Littorinoidea, since few species are known in enough detail to reveal this.

All examined species of **Zerotulidae** lack paraspermatozoa. This was also reported by Reid (1989) from the Lacuninae and Laevilittorininae, the two most “primitive” littorinid subfamilies. Absence of paraspermatozoa among almost all Rissooidea suggested to Reid that their presence is apomorphic for the higher littorinids. Healy (1990) and Warén & Ponder (1991) reported developing paraspermatozoa in the little-known family Provannidae to be “extremely similar to the ‘nurse-cell’ type paraspermatozoa of littorinids.” We therefore favor the view that the production of paraspermatozoa is plesiomorphic and may be suppressed (but perhaps not lost) in these two littorinid subfamilies and the zeratulids.

Frovina indecora, *Trilirata macmurdensis*, *T. sexcarnata*, and possibly *Zerotula stellapolaris* were found to store sperm in the pericardium. We do not know if this is natural or an artifact, and we cannot rule out the possibility that sperm from the female system was pushed through the gonopericardial duct by a violent contraction when the animal was fixed, but this seems unlikely given the large quantities found in some specimens, and in most species, the absence of sperm in other places.

Pericardial sperm storage is known from scattered occurrences in the rissooid-cingulopsoid-littorinoid radiation (Ponder, 1988:149), but in most of these examples, there are modifications involved, e.g., a receptaculum bulging into the pericardium. Such is not the case in *Zerotulidae*, where spermatozoa evidently enter the pericardium via the gonopericardial duct. Sperm storage (not described in detail) in the pericardium occurs also in *Globularia fluctuata* (Sowerby, 1825), which, however, is aphallic (Kase, 1990). No further details about this have been published. (*Globularia* is usually referred to the Naticidae, subfamily Ampulospirinae.) *Campanile symbolicum* Iredale, 1917 (Campanilidae, Cerithioidea) also stores sperm in the pericardium, but in a seminal receptaculum within the pericardium, and opening into the pallial cavity close to the pallial gonoduct (Houbrick, 1981, 1989).

Both the male and female glandular ducts are closed. This has usually been considered an advanced feature among caenogastropods, but Reid (1989) found it to be plesiomorphic in the Littorinoidea. A closed system in the *Zerotulidae* supports this conclusion.

The pedal ganglia have accessory ganglia, a single, anterior one, or two, one anteriorly, one posteriorly. The Littorinidae have two accessory pedal ganglia, one anteriorly, one posteriorly (Johansson, 1939; Fretter & Graham, 1962); the Rissoidae and Hydrobiidae also have two (Johansson, 1939; Hershler & Davis, 1980) in a similar position. We consider the single zerotulid accessory ganglion a synapomorphy of most zerotulids, but the two accessory ganglia in *Dickdellia* may be the plesiomorphic condition.

The osphradium differs from that of the Littorinidae in having the lateral ridges of the same height as the central ridge; in the Littorinidae they are much smaller, ciliated tracts (Johansson, 1939; Taylor & Miller, 1989; Reid, 1989). The rissooid osphradium is quite similar to that of the zerotulids (Johansson, 1939: pl. 3, figs. 3–4). Information about other possibly related taxa is insufficient to allow useful comparison.

We assume a long, slender radula to be a plesiomorphic feature for neotaenioglossates since it occurs also in the Abysochrysidae, Provannidae, and many Cerithioidea, which are generally recognized as being old neotaenioglossate taxa (Houbrick, 1979, 1988; Warén & Ponder, 1991). A hooded rachidian tooth also occurs in the Littorinidae (Reid, 1989) and Cingulopsidae (Ponder & Yoo, 1980). The lateral tooth lacks the "littorinid notch" (Reid, 1989) in all zerotulids, which probably is the plesio-

morphic condition. The gross morphology of the zerotulid radula is most similar to that of Abysochrysidae and Littorinidae. Both these families have a "bare" zone between and no overlap of the inner and outer marginal teeth (see Houbrick, 1979:fig. 8; and Figure 3C, herein). We therefore consider the general morphology of the radula plesiomorphic, while the unusually long cusps and strange outer marginal tooth in *Trilirata* and *Zerotula incognita* are considered apomorphic features.

The radular sac passes through the nerve ring, centrally in the cephalopedal haemocoel and ventral to the esophageal gland, extending as far back as this. Here it may eventually make a short lateral loop. In littorinids it lies coiled in several loops over the gland.

The development of the jaw varies considerably among the zerotulids. So it does also in the whole "rissooid-cingulopsoid-littorinoid radiation" (Reid, 1989), but since a similarly shaped jaw is present in most prosobranchs, little can be concluded from this.

A well-developed esophageal gland is common among Neotaenioglossa; the combination with esophageal pouches is known from the Eatoniellidae, some Cingulopsidae and Littorinidae (Ponder, 1988; Reid, 1989). Esophageal pouches are, however, easily overlooked in serial sections, and therefore they may be more widespread than presently known.

Unusual features of the "rissooid-cingulopsoid-littorinoid radiation," present in zerotulids are:

- Posterior pedal gland large in adult specimens but without large duct (considered an apomorphy of *Zerotulidae*; absent in adult Littorinidae).
- Penis situated below right cephalic tentacle (as in Littorinidae, considered plesiomorphic in Neotaenioglossa).
- Sperm storage in the pericardium (apomorphy of *Zerotulidae*?).
- Absence of a bursa copulatrix (apomorphy of *Zerotulidae*?).
- A long, slender radula with a bare zone between the marginals and with lateral teeth without "littorinid notch" (plesiomorphy of the Neotaenioglossa).
- Presence of a large esophageal gland (plesiomorphy of Neotaenioglossa).
- Presence of esophageal pouches in at least some species (apomorphy of Littorinoidea?).

From this, we conclude that the zerotulids are more closely related to the Littorinidae than to other taxa within the "rissooid-cingulopsoid-littorinoid radiation," and place them in the Littorinoidea. We refrain from comparisons with the pomatiasids and other land and freshwater radiations since we find it difficult to assess differences, which may be caused by their different environment.

We readily admit that there are few and not very clear apomorphies uniting the species included in *Zerotulidae*, and there is a possibility that what we have brought together as *Zerotulidae* actually is a series of unusually

plesiomorphic littorin(o?)ids. In that case, the **Zerotulidae** would be paraphyletic and perhaps polyphyletic. We suspect this especially with *Dickdellia labioflecta*, which differs considerably from the other species in the anatomy of the foot. Nevertheless, if this is the case, there will still remain a need for a family level name based on *Zerotula*, as a sister group to Littorinidae.

The type species of *Skeneopsis* (Skeneopsidae, Littorinoidea), somewhat similar in shell shape to certain zerotulids, was described anatomically by Fretter (1948). Huber (1993) described the central nervous system. The Skeneopsidae includes two North Atlantic species, and shows clear affinity to the Littorinoidea and Cingulopsoidea (Ponder, 1988; Reid, 1989). The single anatomically known species does, however, have a very large penis (pedally innervated, Ponder, 1988) attached behind the right cephalic tentacle, not below, as in Littorinidae and **Zerotulidae**, and it lacks an esophageal gland. Its osphradium is not bipectinate as stated by Fretter (1948), but a low, rather broad ridge, twice as long as broad (Warén, unpublished). The nervous system is highly concentrated.

The Skeneopsidae seems to be a highly apomorphic group and is difficult to place in a superfamily, though the radula and inner chitinous layer of the shell indicate relations to Cingulopsoidea and Littorinoidea, not to Rissooidea. We consider the similarity in shell shape to some zerotulids due to convergence.

Separation of *Frovina*, *Trilirata*, *Dickdellia*, and *Zerotula*:

The soft parts are of very little use in this (except for *Dickdellia*) since they are very featureless, and we have had access to preserved material of only a single species of *Zerotula*. The radula is, however, quite characteristic in the group we have separated as *Trilirata* (plus *Z. incognita*), with an extra cusp halfway up the shaft of the outer marginal tooth combined with a weaker zone across the shaft that causes the tooth to fold here. Also, the shell is quite similar in *T. macmurdensis* and *T. herosae*, whereas that of *T. sexcarinata* has a much more depressed spire. *Trilirata sexcarinata* also stands out among the species of this genus in the extreme development of the periostracum. The periostracum is thin in *Z. stellapolaris* and *Z. incognita*, both in alcohol and dry, but not known in the other species of *Zerotula*. It is thin and brittle in species of *Frovina*. At present we therefore consider the periostracal development of *T. sexcarinata* an autapomorphy.

The two species in *Frovina* which have been examined anatomically have very similar shells, which, however, may be plesiomorphic since they also resemble the shell of unmodified littorinids (Laevilittorininae and Lacuninae).

The shells of the species placed in *Zerotula* are quite similar to each other, but also simple, with a strongly depressed spire, ranging from slightly hyperstrophic via perfectly planispiral to having the larval shell level with the top of the peristome. Several species with similar shells previously classified in *Zerotula* are herein referred to other families.

Frovina Thiele, 1912

Frovina Thiele, 1912:196. Type species *F. soror* Thiele, 1912, by original designation.

Sublacuna Thiele, 1912:195 (not Pilsbry, 1895). Type species *S. indecora* Thiele, 1912, by original designation.

Prolacuna Thiele, 1913:86 (new name for *Sublacuna*).

Frigidilacuna Tomlin, 1930:23 (new name for *Sublacuna*).

Remarks: We cannot see any great differences between the type species of *Prolacuna* and *Frovina*, except the shape of the central tooth, which has only three strong, flat cusps of equal size in *F. soror*, and five conical cusps, which become gradually smaller toward the side of the tooth in *F. indecora* (Figure 3C, E). This was Thiele's only reason for separation of *Frovina* and *Prolacuna*, but we consider the similarities in other radular features, shell, and anatomy more important. Consequently, the name *Frovina* has to be used, since it is the oldest one available.

Prolacuna macmurdensis stands out by its strong spiral sculpture and the strange morphology of the outer marginal tooth, similarities to two new species, and has therefore been united with these in a new genus, *Trilirata*.

Frovina angularis, sp. nov. is classified in *Frovina* with some doubt also at family level; no soft parts were available, but the shell shows more similarities to this family and genus than to any other taxon known to us.

Frovina soror Thiele, 1912

(Figures 1D, E, 2A, B, 3E, F, 4E, F, 6B)

Frovina soror Thiele, 1912:196, pl. 11, fig. 40; pl. 15, fig. 20.

Frovina soror: Egorova, 1982:31, figs. 144, 44.

Prolacuna indecora: Dell, 1990:162 (partly, fig. 239 only).

Type locality: Antarctica, Gauss Station, 89°E, 385 m.

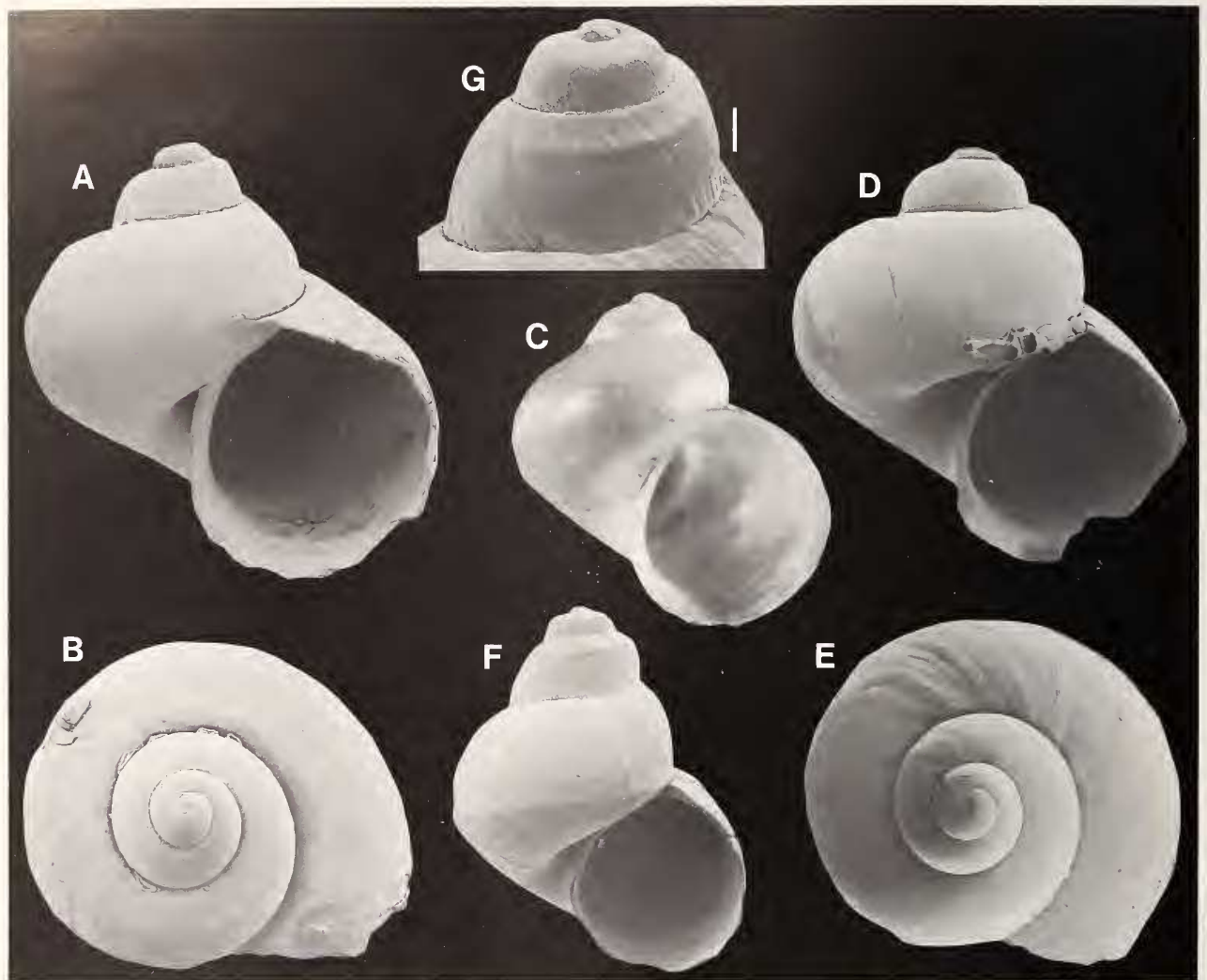
Type material: Holotype in ZMHU, not seen.

Material examined: Davis Sea, 66°33'S, 93°01'W, 80 m, 1 specimen (det. *P. indecora* by Dell, 1990), USNM 613041.—PS VII/4 sta. 224, 013°W, 186–187 m, 2 specimens.—PS VII/4 sta. 274, 012°W, 196–212 m, 5 specimens.—PS IX/3, sta. 173, 007°E, 739–765 m, 5 specimens, 2 shells.—PS IX/3, sta. 174, 011°E, 432–432 m, 10 specimens, 4 shells.—PS IX/3, sta. 179, 007°E, 185–161 m, 2 specimens, 9 shells.—PS IX/3, sta. 180, 06°E, 280–298 m, 17 specimens, 3 shells.—PS IX/3, sta. 206, 10°E, 343–338 m, 2 specimens, 10 egg capsules, 3 shells.—PS IX/3, sta. 211, 05°E, 661–742 m, 3 shells (all in SMNH).

Distribution: From the Bellinghausen Sea (93°W), eastward to the Davis Sea (98°E), in 80–765 m.

Redescription: We describe only the anatomy, based on several decalcified specimens and sections of one adult female. Shell, Figure 1D, E; protoconch, Figure 2A, B.

External morphology of soft parts: The head-foot and pallial complex comprise half a whorl in contracted spec-

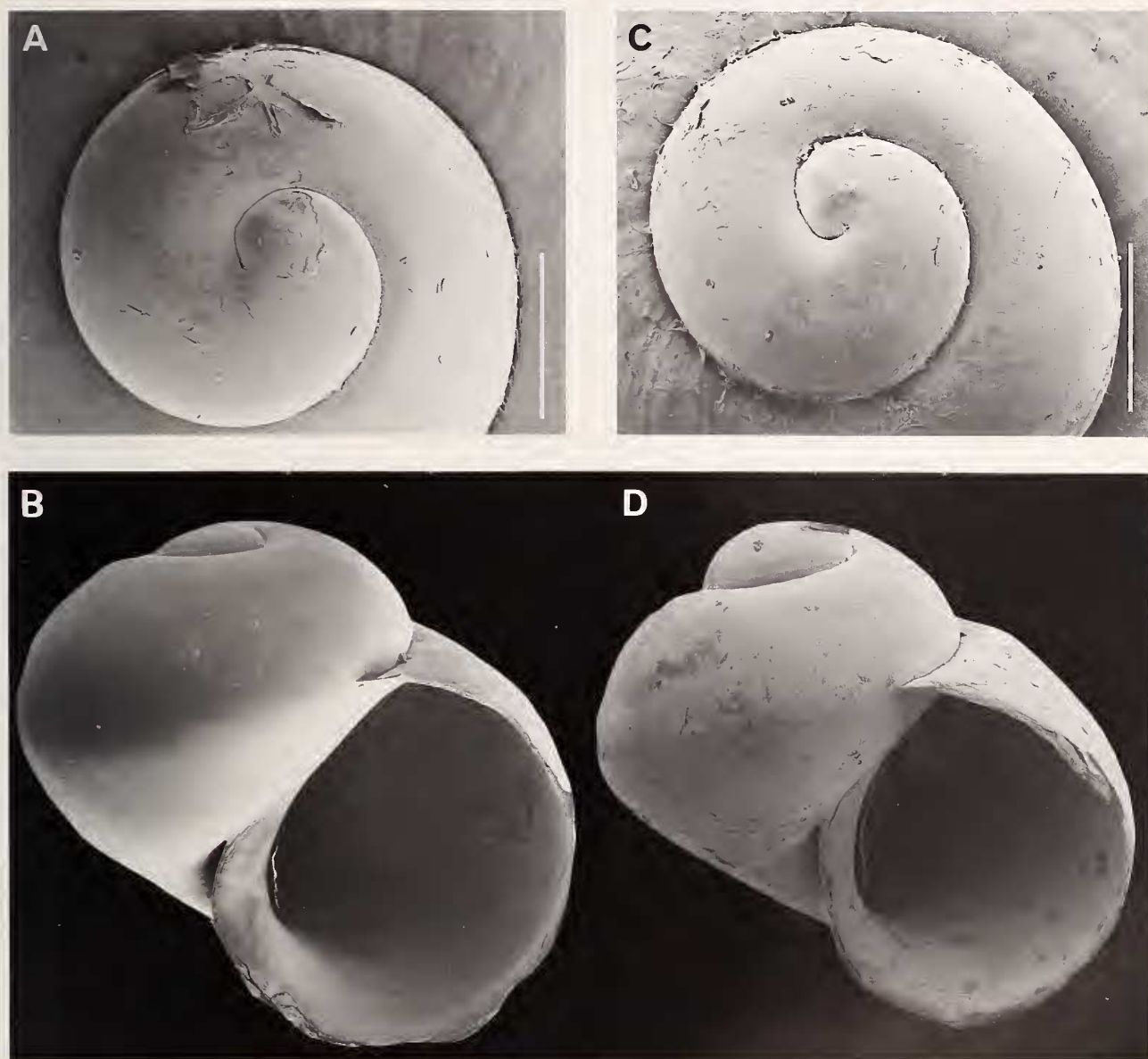


Explanation of Figure 1

Frovinia spp. Figures A, B. *F. indecora*, PS IX/3 sta. 179, height 3.4 mm. Figure C. *F. indecora*, holotype, ZMHU 63025, height 2.3 mm. Figures D, E. *F. soror*, USNM 613041, height 3.3 mm and (E) PS IX/3 sta. 179, diameter 3.2 mm. Figures F, G. *F. angularis* Warén & Hain, sp. nov., holotype, height 3.2 mm. Scale line (G) = 0.2 mm.

imens, the visceral mass slightly more than two whorls. The head-foot is pale beige, the visceral mass pale orange-brown (in alcohol) and covered with small dark brown spots, diameter about 5–15 μ m. The anterior $\frac{1}{10}$ whorl of the visceral mass is dominated by the still paler kidney. At the left side, the pericardium with the ventricle and auricle lies directly behind the gill and osphradium. The gonad is not easily distinguished externally, although the specimens are sexually mature. Directly behind the pericardium, the esophagus and stomach reach about a third of a whorl backward, before the esophagus enters the posteriorly situated part of the stomach. Forming a continuation of the anteriorly situated part of the stomach, the intestine very soon turns sharply to the right and disappears under the kidney.

The pallial cavity is quite deep, and the pallial skirt normally covers the whole head in preserved specimens. The pallial margin is thin and simple, without tentacles and papillae, except at the right $\frac{1}{2}$, where it is "uneven," but the details could not be worked out. The osphradium is elongate and paralleled by two ciliated ridges. It runs along the gill from its most posterior part, forward to the anterior $\frac{1}{4}$ of the gill. The gill consists of a series of about 12 triangular leaflets, drawn out to a ventral point; the gill width corresponds to $\frac{1}{4}$ of the pallial cavity. The leaflets in its central part are about twice as wide and high as the anterior ones. The columellar muscle projects at the right side of the body, 80–100° from the operculum. Its left part is much less conspicuous and narrower. The hypobranchial gland is not very conspicuous and partly covered by the



Explanation of Figure 2

Frovina spp., juveniles. Figures A, B. *F. soror*, PS IX/3 sta. 179, diameter 1.1 mm. Figures C, D. *F. indecora*, PS IX/3 sta. 179, diameter 1.1 mm. Scale lines = 250 μ m.

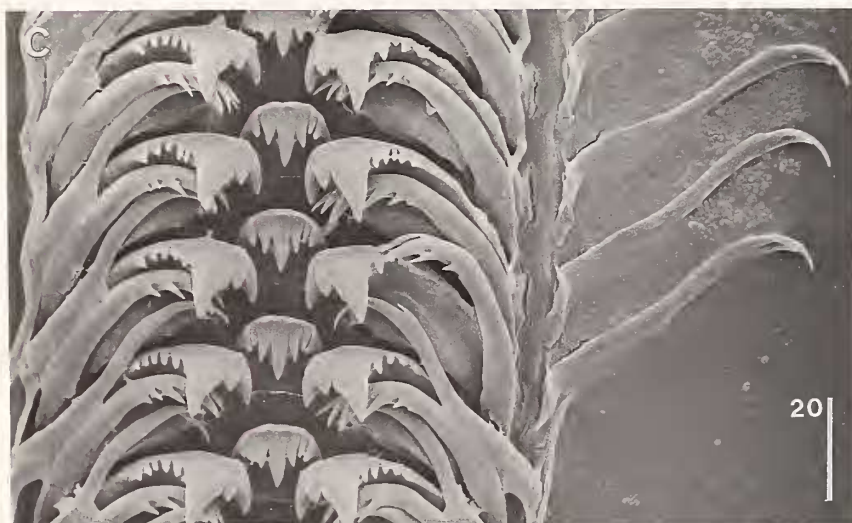
tips of the gill leaflets. The pallial oviduct is restricted to the posterior right half of the cavity, and its left side contains the rectum, which opens at the same level as the duct.

The head is medium-sized, has a pair of short (contracted), conical, flattened tentacles with large, black eyes in basal-lateral bulges. The snout is rather short, slightly tapering, and somewhat flattened with a subventral mouth.

The male has a simple, tapering, finger-shaped penis just below the right cephalic tentacle, with a seemingly open furrow along its dorsal side. The furrow continues as a duct buried in the right corner of the pallial cavity, to the prostate.

The foot is flat, large, and broad. It is strongly contracted in all specimens, but judging from the folds, its anterior edge is probably blunt, and the corners are not drawn out to small, tentaclelike extensions. Posteriorly, it seems bluntly rounded. An anterior pedal gland opens between the indistinctly set-off propodium and the mesopodium. The sides of the foot are smooth and there are no epipodial ridges or furrows.

Internal anatomy: The foot is almost filled by the large posterior pedal gland, which, together with the slightly smaller anterior pedal gland, bulges into the cephalopedal



Explanation of Figure 3

Radulae of *Zerotula* and *Frovina*. Figures A, B. *Z. hedleyi*, MNZ M.33660. Figures C, D. *F. indecora*, PS IX/3 sta. 180. Figures E, F. *F. soror*, USNM 613041. Scale lines in μm .

haemocoel, well past the nerve ring, both to the right and left of it. The posterior pedal gland stains dark bluish violet, the anterior one, a much lighter grayish violet. The posterior pedal gland seems not to have a defined opening, but this is not certain, because all the ventral surface of the foot is badly preserved, and the outer layers are peeling. The anterior one has a storage space under the propodium lined with tall epithelium, and opens via the slit between the pro- and mesopodium. The muscle layer of the foot is quite thin, 30–60 μm along the sides and ventrally, and the sole is very poor in muscle fibers.

The tentacles are solid and muscular, all the way to the base, where they have a subcutaneous eye with lens and pigment layer, in a bulge. The snout is very muscular and can probably be extended considerably when the snail is grazing.

The alimentary system consists of the mouth, a large, rather weakly muscular buccal mass, a very short anterior esophagus, a large esophageal gland, a narrow posterior esophagus, stomach, intestine, and rectum. From the posterior esophagus and backward, the preservation was too poor to observe any detail, except that the stomach has a gastric shield but seems to lack a crystalline style.

The jaw is very thin and membranous, mainly forming a cuticular lining of the oral tube.

The radular sac is straight, long, and slender, passes backward through the nerve ring and lies ventral to the esophageal gland as far back as this. The part of the radula in use is supported by a pair of narrow cartilages.

Two salivary glands open into the buccal cavity, close to its mid-line, via short, inconspicuous ducts, which do not pass through the nerve ring. The salivary glands are large and situated in front of and above the cerebral ganglia. They consist of a short, thin duct and a longer, coiled and branching glandular tube. Their structure and staining are very similar to the dorsal part of the esophageal gland, but the nuclei are more numerous and conspicuous. The dorsal food channel is characterized by the presence of numerous mucus-producing cells, which stain dark blue. These start in the postero-dorsal part of the buccal cavity, are displaced to the left when passing the nerve ring, and end up ventrally in the esophageal gland, where they do not reach its posterior end. A paired structure (about 0.2 mm long), which could be a pair of esophageal pouches, bulges from the esophagus, just in front of the gland.

The nervous system follows the normal pattern, with dialyneurys between the left pleural and the supraesophageal ganglia. The distances between the ganglia are fairly short (contracted specimen). The left pleural and cerebral ganglia are partly fused, the right ones abutting. The supra- and subesophageal ganglia are situated less than twice their diameter from the corresponding pleural ganglion. The length of the connectives to the pedal ganglia is twice the diameter of the ganglia. The supraesophageal ganglion lies free at the left side of the cephalopodal haemocoel; the subesophageal one is well embedded in the body wall. The

buccal ganglia are situated dorsally on the buccal mass, close to the exit of the esophagus, and connected by a commissure. In front of the pedal ganglia is an accessory pedal ganglion, lying in the anterior pedal gland, connected by a connective of 1.5 times the diameter of the accessory ganglion and innervating the anterior pedal gland and propodial area. The visceral ganglia were not identified.

The statocysts are situated above and behind the pedal ganglia and slightly displaced to the right. Their diameter corresponds to $\frac{1}{3}$ of the length of the ganglion. They have a single statolith.

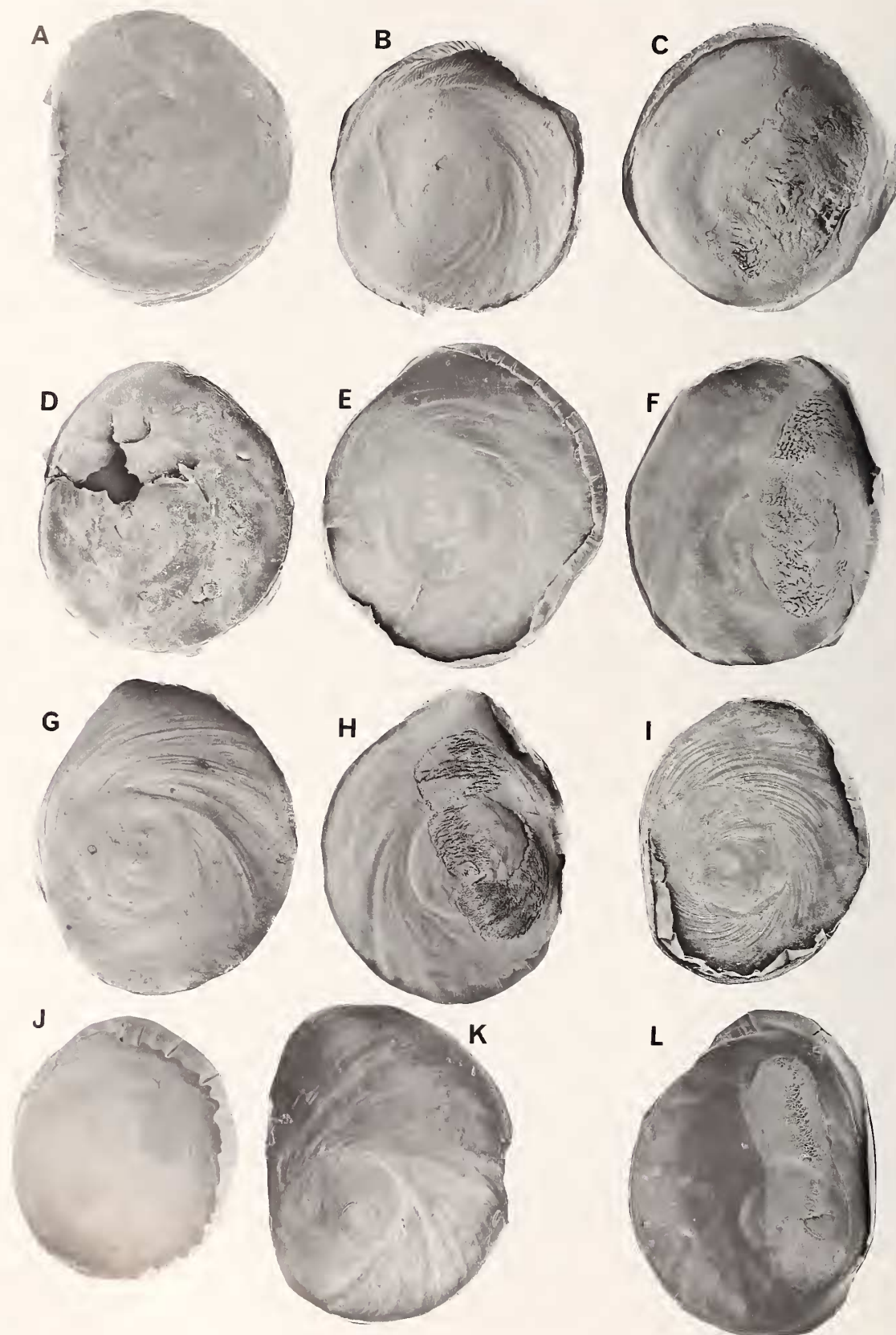
Reproductive system. The sexes are separate, or at least the males whose external morphology was examined were of the same size as the sectioned female. The fixation does not allow any detailed description of the female system. The ovary (and testis) lie along the right side of the visceral mass. An ovarian duct leads to a large albumen gland, which stains very lightly. Along the left and anterior side of this is a capsule gland (staining dark violet), but the detailed morphology of these could not be worked out due to missing and ruptured sections. No bursa copulatrix was identified. No receptaculum seminis was found, and no sperm was found in the pericardium.

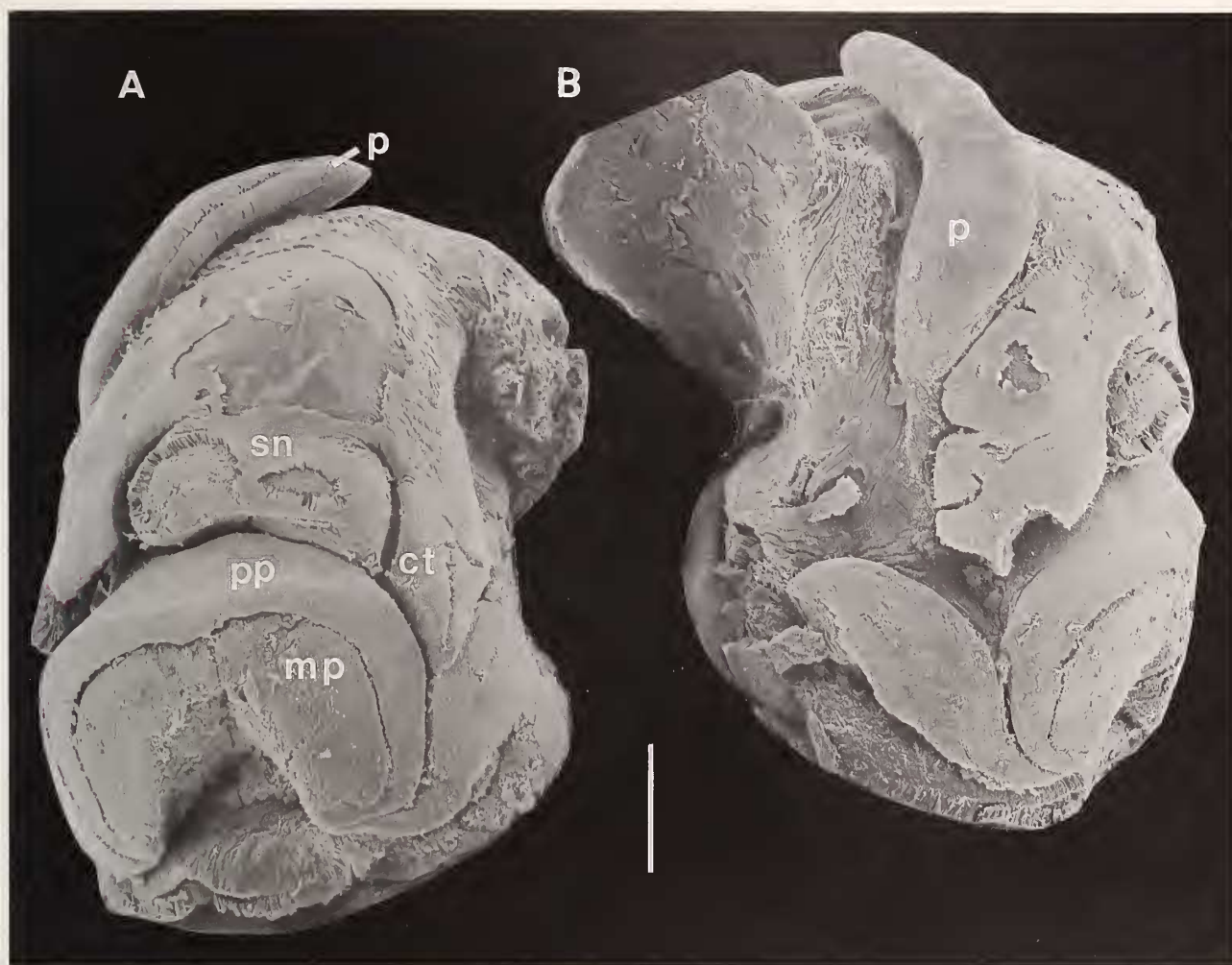
The radula (Figures 3E, F, 6B) is taenioglossate, long, and slender, with about 80 transverse rows of teeth. The central tooth (Figure 3F) has a low and thin, irregularly denticulated hood along its anterior, apical margin. Below this, three large cusps form a cutting edge. Beside these, and partly concealed by them, is a much smaller denticle on each side. The “wings” are drawn out to a small denticle on each side close to the base. The front of the tooth forms a large supporting bulge at the base. The lateral tooth usually has about 10 denticles, of which numbers 2 and 4 (counted from the inner edge) are at least twice the size of the others. The littorinid notch is missing. The first marginal tooth is simple, claw-shaped, with a sturdy shaft and three to five apical cusps. The outer marginal tooth is slightly shorter, straighter, half the thickness, and has three apical cusps. Very young specimens (from egg capsules) have a proportionally shorter radula with fewer transverse rows of teeth, but the radulae are otherwise identical.

The operculum (Figure 4E, F) has a few whorls, a central nucleus, and is transparent, slightly brownish yellow, especially where it is attached to the foot. The surface is distinctly wrinkled by the growth lines.

Reproduction. The egg capsules are identical to those described for *F. indecora* below.

Remarks: *Frovina soror* was based on a small specimen, 1.5 mm high and 1.4 mm in diameter. Thiele's drawing of the shell (1912: pl. 11, fig. 40) is not much of an aid to identification, but the radula is distinctive (Thiele, 1912: pl. 15, fig. 20), even in juveniles (Figure 6B, from egg capsules) with three large cusps of equal size on the central





Explanation of Figure 5

Frovina indecora, critical point dried, PS IX/3 sta. 212. Figure A. front view. Figure B. right side of head-foot. ct—cephalic tentacle, mp—mesopodium; p—penis with sperm groove; pp—propodium; sn—snout. Scale line = 200 μ m.

tooth. Our material indicates a size of a little more than 3 mm for adult specimens.

Neither sperm nor a receptaculum seminis was found in the single sectioned female. The reason is probably that it had not been fertilized, because the sections were good enough to find a filled receptaculum or sperm in the pericardium.

Frovina indecora (Thiele, 1912)

(Figures 1A–C, 2C, D, 3C, D, 4G, H, 5, 6A, 7, 8, 9, 22D)

Sublacuna indecora Thiele, 1912:195, pl. 12, fig. 4; pl. 15, fig. 19.

Prolacuna indecora: Arnaud, 1972:126.

Prolacuna indecora: Egorova, 1982:30, fig. 142–143, 42.

Explanation of Figure 4

Opercula. Figure A. *Zerotula hedleyi*, MNZ M.33660, diameter 0.40 mm. Figures B, C. *Z. stellapolaris* Warén & Hain, sp. nov., PS IX/3 sta. 180, diameter 0.68 mm. Figure D. *Z. sp.*, Bounty Trough, diameter 0.85 mm. Figures E, F. *Frovina soror*, PS IX/3 stas. 179 and 180, diameter 1.8 and 1.9 mm. Figures G, H. *F. indecora*, PS IX/3 sta. 179 and 180, diameter 2.1 and 1.9 mm. Figure I. *Trilirata macmurdensis*, USNM 612745, diameter 1.6 mm. Figure J. *T. herosae* Warén & Hain, sp. nov., holotype, diameter 1.7 mm. Figures K, L. *T. sexcarinata* Warén & Hain, sp. nov., PS VII/4 sta. 291 and 284, 1.7 and 1.6 mm.





Explanation of Figure 7

Frovina indecora, longitudinal section. The pedal ganglion has just branched to two major tracts (indicated by arrows), to the accessory pedal ganglion and to the posterior region of the mesopodium. **cg**—cerebral ganglion; **df**—dorsal (now ventral) food channel; **f**—foot; **j**—jaw; **oe**—esophagus; **oep**—esophageal pouch; **pc**—pallia cavity; **pg**—pedal ganglion; **plg**—pleural ganglion; **pp**—propodium; **sg**—salivary gland; **sn**—snout. Scale line = 100 μ m.

Prolacuna indecora: Powell, 1951:121.

Trochacis antarctica: Powell, 1958:185, not Thiele, 1912.

Prolacuna indecora: Powell, 1958:190.

Prolacuna indecora: Dell, 1990:162 (not fig. 239, = *Frovina soror*).

NOT *Sublacuna indecora* Eales, 1923:21 (= unidentified naticid).

Type locality: Davis Sea, Gauss Station, 89°E, 385 m.

Type material: Syntype ZMHU 63025, examined.

Material examined: PS VII/4 sta. 284, 013°W, 402–412 m, 2 specimens.—PS VII/4 sta. 274, 012°W, 196–212 m,

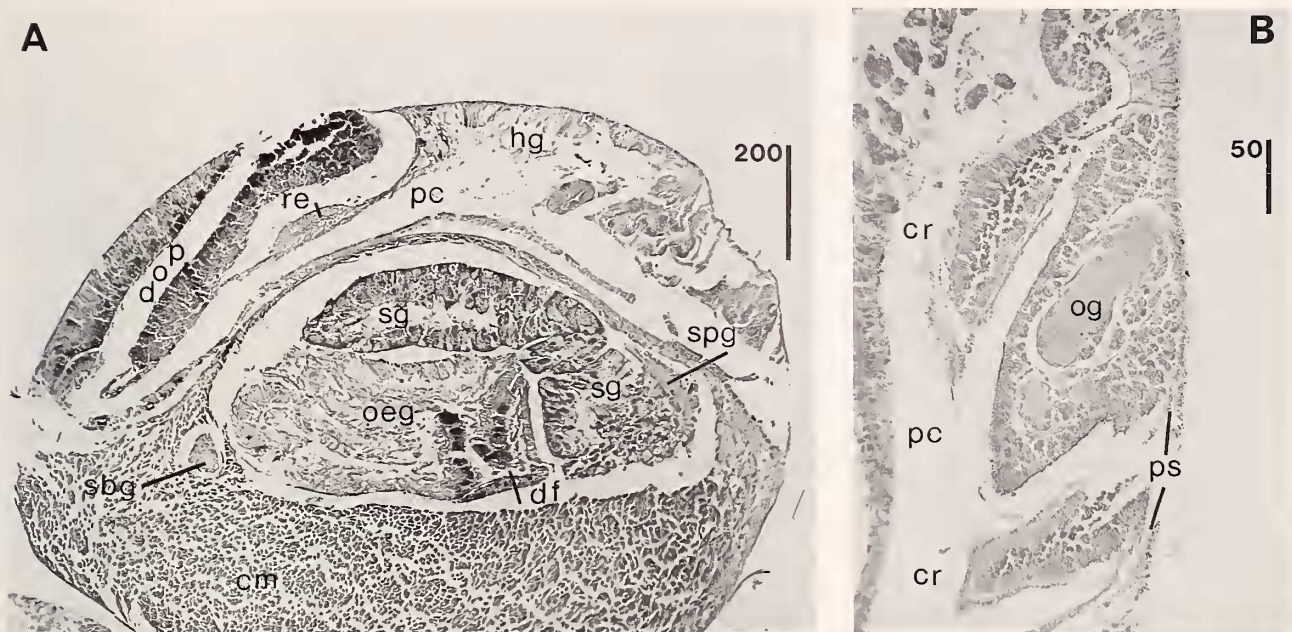
6 shells.—PS IX/3, sta. 165, 003°W, 191–204 m, 2 shells.—PS IX/3, sta. 173, 007°E, 739–765 m, 33 specimens, 5 shells, 14 egg capsules.—PS IX/3, sta. 174, 010°E, 432–432 m, 2 specimens.—PS IX/3, sta. 179, 007°E, 185–161 m, 14 specimens, 10 egg capsules, 21 shells.—PS IX/3, sta. 180, 006°E, 280–298 m, 26 specimens, 15 egg capsules, 4 shells.—PS IX/3, sta. 206, 010°E, 343–338 m, 2 specimens, 3 shells.—PS IX/3, sta. 211, 005°E, 661–742 m, 1 specimen, 2 shells.—PS IX/3, sta. 212, 003°E, 568–644 m, 15 specimens, 5 egg capsules (all in SMNH).

Distribution: Circumpolar in 67–836 m.

Explanation of Figure 6

Figure A. *Frovina indecora* juvenile, from Figure 2D, PS IX/3 sta. 179. Figure B. *F. soror* juvenile, from Figure 2B, PS IX/3, sta. 179. Figures C–F. *Trilirata macmurdensis*, PS IX/3, sta. 173. C. Juvenile, from Figure 34F. D–F. Adult to show central tooth and folding of outer marginals. Scale lines = 5 μ m.





Explanation of Figure 9

Frovina indecora. Figure A. Cross section of body behind cerebral ganglia, to show position of esophageal ganglia. Figure B. Cross section of osphradium. **cm**—columellar muscle; **cr**—ciliated ridge; **df**—dorsal food channel; **hg**—hypobranchial gland; **oeg**—esophageal gland; **og**—osphradial ganglion; **pc**—pallial cavity; **pod**—pallial oviduct; **ps**—pallial skirt; **re**—rectum; **sbg**—subesophageal ganglion; **sg**—salivary gland; **spg**—suprasophageal ganglion. Scale lines in μm .

Redescription: We only describe the anatomy, based on three sectioned adult females and several decalcified males and females. Shell, Figure 1A–C; protoconch, Figure 2C, D.

External morphology of soft parts: The head-foot (Figure 5) and pallial complex comprises $\frac{2}{3}$ of a whorl in a contracted specimen, the visceral mass slightly more than two whorls. The anterior part of the head-foot has a weak, granular, grayish pigmentation, best visible along the edges of the snout, foot, and tentacles. Behind the tentacles, including the visceral mass, it is light beige (in alcohol). The anterior $\frac{1}{10}$ whorl of the visceral mass is yet paler and contains the kidney. At the left side, the pericardium, with the ventricle and auricle, lies directly behind the gill and osphradium. The gonad is not easily distinguished externally also in sexually mature specimens. Directly behind

the pericardium, the esophagus and stomach reach about a third of a whorl backward, before the esophagus enters the posteriorly situated part of the anterior stomach. Forming a continuation of the anteriorly situated part of the stomach, the intestine very soon turns sharply to the right and disappears under the kidney.

The pallial cavity is quite deep, and the pallial skirt normally covers the whole head in preserved specimens. The pallial margin is thin and simple, without tentacles and papillae, except at the right $\frac{1}{2}$, where it is "uneven," but the details could not be worked out. The osphradium (Figure 9B) is paralleled by two ridges; it runs along the gill from its most posterior part, forward to the anterior $\frac{1}{4}$ of the gill. The gill consists of a series of about 12 triangular leaflets, drawn out to a ventral tip; the gill width corresponds to $\frac{1}{4}$ of the pallial cavity. The leaflets in its

Explanation of Figure 8

Frovina indecora, sagittal sections. Figure A. Longitudinal section of central anterior part of cephalopodal haemocoel. Figure B. Longitudinal section through head-foot, changing to cross section of anterior part of visceral mass. **ag**—albumen gland; **apg**—anterior pedal gland; **cc**—cerebral commissure (in B indicated by black dot and fine arrow); **cm**—columellar muscle; **df**—dorsal (now ventral) food channel (visible by its dark staining gland cells); **dg**—digestive gland; **fp**—fecal pellet (in rectum); **m**—mouth; **oe**—esophagus; **oeg**—esophageal gland; **oev**—esophageal valve; **pod**—pallial oviduct; **pp**—propodium; **rc**—radular cartilage; **rs**—radular sac; **sd**—salivary duct; **st**—stomach. Scale lines in μm .

central part are about twice as wide and high as the anterior ones. The columellar muscle projects at the right side of the body, 80–100° from the operculum. Its left part is much less conspicuous and narrower. The hypobranchial gland is rather inconspicuous and partly covered by the tips of the gill leaflets. The pallial oviduct is restricted to the posterior right half of the cavity, and its left side contains the rectum, which opens at the same level as the duct. In the male, the rectum parallels the sperm duct and prostate in the corresponding position.

The head is medium-sized and has a pair of short (contracted), conical, flattened tentacles with large black eyes in basal-lateral bulges. The snout is rather short, with parallel sides, somewhat flattened with a subventral mouth.

The male has a simple, tapering, finger-shaped penis just below the right cephalic tentacle, with a dorsal furrow containing a closed sperm duct. The duct continues in the right corner of the pallial cavity, lined by a narrow prostate gland.

The foot is flat, large, and broad. Judging from the folds, its anterior edge is probably blunt, but the corners seem not to be drawn out to small, tentaclelike extensions. Posteriorly, it seems bluntly rounded. There is no distinct opening for the posterior pedal gland. Anteriorly, between the distinctly set-off propodium and the mesopodium, opens an anterior pedal gland. The sides of the foot are smooth, and there are no epipodial ridges or furrows.

Internal anatomy (Figures 7–9): The foot (Figure 8B) is almost filled by the large posterior pedal gland. The slightly smaller anterior pedal gland bulges into the cephalopodal haemocoel, but not behind the nerve ring. The posterior pedal gland stains dark bluish violet, the anterior one a much lighter grayish violet with conspicuous nuclei. The posterior pedal gland does not have a defined opening. The anterior one has a storage space under the propodium lined with tall epithelium, and opens via a broad and flat duct, which penetrates most of the gland. The muscle layer of the foot is quite thin, 75–100 μm along the sides and ventrally.

The tentacles are solid and muscular all the way to the base, where they have a subcutaneous eye with lens and pigment layer, in a bulge. The snout is very muscular and can probably be extended considerably when the snail is grazing.

The alimentary system consists of the mouth; a large, rather muscular buccal mass; a very short anterior esophagus; a large esophageal gland; a narrow posterior esophagus; stomach; intestine; and rectum. From the posterior esophagus and backward, the preservation was too poor for any detail except that the stomach has a gastric shield but seems to lack a crystalline style.

The jaw (Figure 22D) is bilobed and thin but with a prismatic structure.

The radular sac (Figure 8A) is straight, long, and slender, passes backward through the nerve ring and lies ventral to the esophageal gland, reaching as far back as this, where it curves dorsally to the right of the esophagus. The

part of the radula in use is supported by a pair of large cartilages.

Two salivary glands open into the buccal cavity close to its mid-line, via short, inconspicuous ducts which do not pass through the nerve ring. The salivary glands are large and situated in front of and above the cerebral ganglia. Each consists of a short, thin duct and a voluminous gland of several lobes. With EHE they stain violet. The dorsal food channel (Figures 7, 8A) is characterized by the rich occurrence of mucus-producing cells, staining dark blue. These start in the posterior, dorsal part of the buccal cavity, get displaced toward the left side when passing the nerve ring and end up ventrally in the esophageal gland, where they do not reach its posterior end. In front of the esophageal gland is a pair of small esophageal pouches.

The nervous system follows the normal pattern of littorinids, with dialyneury between the left pleural- and the supraesophageal ganglia. The distances between the ganglia are fairly short (contracted specimen), the pleural and cerebral ganglia abutting. The supra- and subesophageal ganglia are situated less than twice their diameter from the corresponding pleural ganglion. The length of the connectives to the pedal ganglia is twice the diameter of these ganglia. The supraesophageal ganglion lies free at the left side of the cephalopodal haemocoel; the subesophageal one in a pit in the body wall (Figure 9A). The buccal ganglia are situated dorsally on the buccal mass close to the exit of the esophagus, and connected by a commissure. In front of the pedal ganglia is an accessory pedal ganglion, connected by a connective of the same length as the accessory ganglion and innervating the anterior pedal gland and propodial area.

The visceral ganglia were not identified.

The statocysts are situated above and behind the pedal ganglia and slightly displaced laterally. Their diameter corresponds to half the length of the ganglion. They have a single statolith.

Reproductive system. The sexes are separate. The fixation does not, however, allow any detailed description. The gonad lies along the right side of the visceral mass. An ovarian duct leads to a large albumen gland, which stains very lightly. Along the left and anterior side of this is a capsule gland (staining dark violet with EHE), but the detailed morphology of these could not be worked out due to missing and ruptured sections. They are, however, closed except for a short opening close to the anterior end of the capsule gland. No trace of a bursa copulatrix or a receptaculum seminis was found. A well-developed gonopericardial duct is present, opening into the ovarian duct close to the albumen gland. All three females that were sectioned had the pericardium filled with sperm.

The radula (Figures 3C, D, 6A) is taenioglossate, long, and slender, with about 100 transverse rows of teeth. The central tooth (Figure 3D) has a low and thin, irregularly crenulated hood along its apical margin. Below this, one large and two smaller cusps form a cutting edge on each side. Beside these, and partly concealed by them, is a much smaller denticle on each side. The "wings" are not drawn

out to small denticles on the sides. The front of the tooth forms a large supporting bulge at the base. The lateral tooth usually has seven or eight denticles, of which numbers 1 and 3 or 4 (counted from the inner edge) are at least twice the size of the others. The littorinid notch is missing. The first marginal tooth is simple, claw-shaped, with a sturdy shaft and three to five large apical cusps. The outer marginal tooth is longer and of a fourth of the thickness of the inner one. It has two or three apical cusps. Very young specimens have a proportionally shorter radula with fewer transverse rows of teeth, otherwise identical (Figure 6A).

The operculum (Figure 6G, H) has a few whorls, a central nucleus, and is transparent, pale brownish yellow, more distinctly so where attached to the foot. The surface is distinctly wrinkled by the growth lines.

Reproduction. The egg capsules are laid singly and contain one embryo. The capsules are globular, transparent, slightly yellowish, and attached to some firm substrate along a surface corresponding to a sector of 60–90° of the sphere. The young snails have a diameter of 1 mm at hatching, and the shell consists of 1.5 whorls. The development is thus lecithotrophic and encapsulated. These may be the unidentified egg capsules reported by Hedgpeth (1964) on legs of the pycnogonid *Colossendeis megalonyx* Hoek, 1881, at the northern part of the Antarctic Peninsula.

Remarks: Eales (1923) outlined some anatomical characters of a species identified as "*Prolacuna indecora*." The description contains details about a "partly calcareous operculum" and "coalescence of tentacles in the mid-dorsal line." She also figured a radula (fig. 26b). On the basis of this, she placed *Prolacuna* in the Naticidae, a position maintained by later authors (Dell, 1990; Kabat, 1991). The information presented, especially the presence of a calcareous layer on the operculum, makes it obvious that she had examined a young naticid, not *Prolacuna indecora*, which lacks calcareous deposits on the operculum.

Examination of one of Powell's (1958) specimens of "*Trochaclis antarctica*" (from Banzare sta. 41, off Enderby Land, the only one that still could be found) showed that it was misidentified and the record was based on *F. indecora*. Dell (1990:fig. 239) figured *Frovina soror* as *P. indecora*.

Frovina indecora is very similar to *Frovina soror*, but adult specimens can be distinguished by *F. soror* having a wider umbilicus and a slightly blunter apex. Access to specimens of both species for comparison is imperative. We recommend that identification of these species be verified by radular examination.

Frovina angularis Warén & Hain, sp. nov.

(Figure 1F, G)

Type locality: BIOCAL station DW70, off southern New Caledonia, 23°25'S, 167°53'E, 965 m.

Type material: Holotype and 1 paratype (the latter from BIOCAL DW51) in MNHN.

Material examined: The holotype and BIOCAL station DW51, off southern New Caledonia, 23°05'S, 167°45'E, 680–700 m, 1 shell.

Distribution: Only known from south of New Caledonia in 680–965 m (shells only).

Etymology: "*angularis*" (Latin) meaning angular, from the appearance of the protoconch.

Description: Shell (Figure 1F) small, rissoidlike, with an angular appearance, grayish semitransparent. The protoconch (Figure 1G) is not distinctly demarcated and has slightly more than 1.5 whorls of a diameter of 1.0 mm. Apically it is distinctly flattened with a successively stronger keel, which demarcates a subsutural shelf. The teleoconch has 1.5–2.0 whorls, demarcated from the protoconch mainly by the gradual weakening of the protoconch keel. It is sculptured by a few, very indistinct spiral lines, a stronger peripheral spiral rib, and scattered prosocline incremental lines. The umbilicus is narrow but deep. The aperture is rounded; the outer lip prosocline.

Dimensions. Height of shell 3.2 mm (paratype slightly smaller).

Remarks: *Frovina angularis* is a featureless shell, and the classification in *Frovina* is provisional in the absence of soft parts. Also, the placement in *Zerotulidae* is based more on intuition and absence of other alternatives than on actual synapomorphies.

Trilirata Warén & Hain, gen. nov.

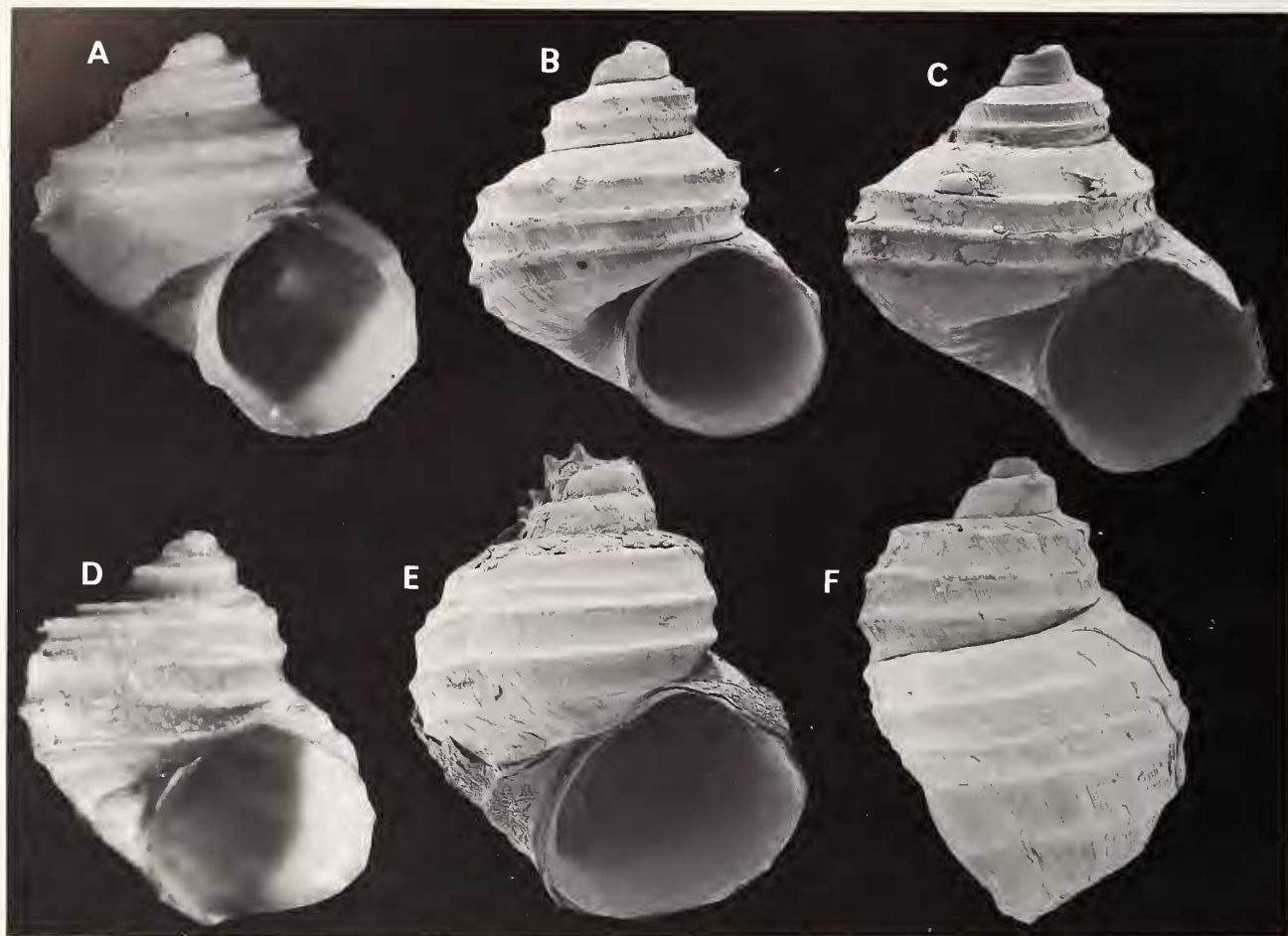
Type species: *Sublacuna trilirata* Thiele, 1912 (= *Lacuna macmurdensis* Hedley, 1911).

Diagnosis: Shell of medium to large size for family, of moderate height or planispiral, mainly sculptured by spiral keels. Protoconch poorly demarcated but indicating lecithotrophic development (known in *T. macmurdensis*). Soft parts as for family. Outer marginal tooth of radula with thin, flat cusp and weak zone halfway up the shaft.

Etymology: "*trilirata*" (Latin), with three spiral cords, also the specific name of the type species.

Remarks: Our reasons for introducing this new generic name were presented under the family heading. We have preferred to select *S. trilirata* as nominal type species since our material is more similar to Thiele's specimens than those of Hedley (although we consider them synonyms).

The four species included in *Trilirata* look quite different when shells only are considered and had we not had some information about anatomy and radula they would have been difficult to classify. The relationship to *Frovina* and *Zerotula* is not obvious from the shell morphology. At the same time, their shell morphology does not easily fall into other families, except *T. sexcarinata*, which easily



Explanation of Figure 10

Trilirata macmurdensis and *Laeviltorina wandelensis*. Figure A. *T. macmurdensis* (holotype of *T. trilirata*), ZMHU 63024, height 3.3 mm. Figure B. *T. macmurdensis*, USNM 612745, height 3.4 mm. Figure C. *T. macmurdensis*, PS IX/3 sta. 179, height 3.1 mm. Figure D. *L. wandelensis* (holotype of *Lacuna notorcadensis*, RSM 1921.143.623, height 3.0 mm. Figures E-F. *L. wandelensis* (paratype of *L. notorcadensis*) NMWZ 1955.158.157, height 3.6 mm.

could have been classified in the Capulidae from the shape of the shell and the development of the periostracum.

Trilirata macmurdensis (Hedley, 1911)

(Figures 4I, 6C-F, 10A-C, 11A-C, 12, 34F, G)

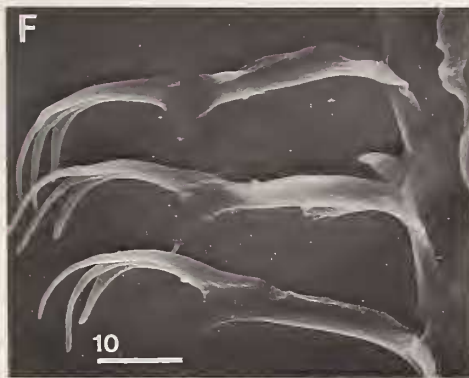
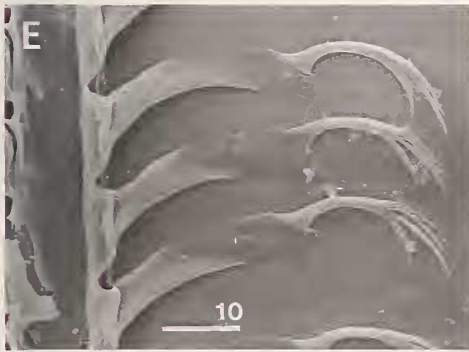
Lacuna macmurdensis Hedley, 1911:4. pl. 1, fig. 6.
Sublacuna trilirata Thiele, 1912:196, pl. 12, fig. 5.

Prolacuna macmurdensis: Arnaud, 1972:126.
Prolacuna trilirata: Egorova, 1982:30, fig. 141.
Prolacuna macmurdensis: Powell, 1951:121.
Prolacuna trilirata: Powell, 1958:190.
Prolacuna macmurdensis: Powell, 1958:191.
Prolacuna macmurdensis: Dell, 1990:163, fig. 258.

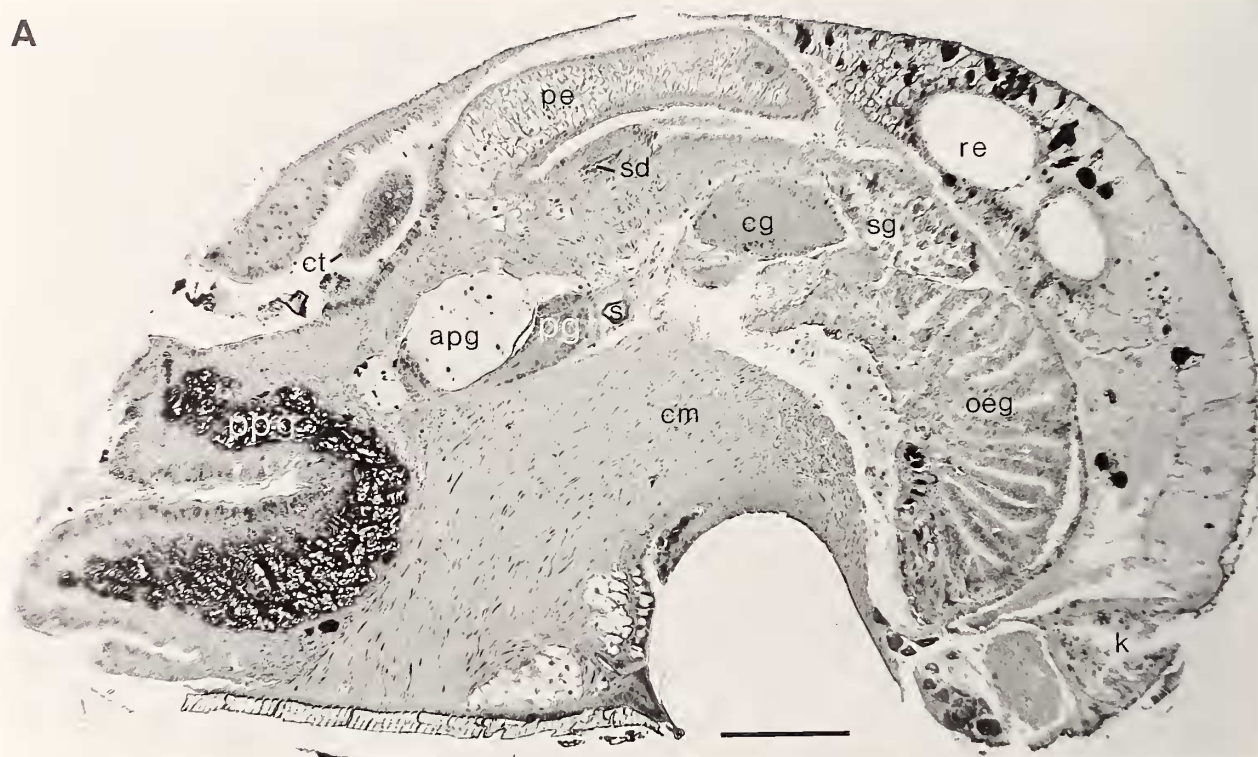
Type localities: *L. macmurdensis*, off Cape Royds, Macmurdy Sound, Ross Sea, 18–36 m: *S. trilirata*, Davis Sea, GAUSS Station, 89°E, 385 m.

Explanation of Figure 11

Radulae of *Trilirata* spp. Figures A-C. *T. macmurdensis*. A. Central tooth. B. Complete width of radula. C. Detail of outer marginal tooth. Figures D, E. *T. herosae* Warén & Hain, sp. nov., holotype. F, G. *T. sexcarinata* Warén & Hain, sp. nov., PS VII/4, sta. 291. Scale lines in μm .



A



B



Type materials: *L. macmurdensis*, in AMS, not examined; *S. trilirata*, syntype ZMHU 63024, examined.

Material examined: PS VII/4, sta. 224, 013°W, 186–187 m, 1 specimen, 3 shells.—PS VII/4, sta. 230, 027°W, 270–280 m, 1 shell.—PS VII/4, sta. 274, 012°W, 196–212 m, 1 shell.—PS VII/4, sta. 289, 013°W, 672 m, 1 specimen.—PS IX/3, sta. 165, 003°W, 191–204 m, 5 shells.—PS IX/3, sta. 173, 007°E, 739–765 m, 3 specimens, 12 shells.—PS IX/3, sta. 174, 010°E, 432–432 m, 6 shells.—PS IX/3, sta. 179, 007°E, 185–161 m, 5 specimens, 5 shells.—PS IX/3, sta. 180, 006°E, 280–298 m, 32 specimens, 5 shells.—PS IX/3, sta. 206, 010°E, 343–338 m, 1 specimen, 1 shell.—PS IX/3, sta. 207, 005°E, 213–210 m, 1 shell.—PS IX/3, sta. 211, 005°E, 661–742 m, 3 shells.—PS IX/3, sta. 212, 003°E, 568–644 m, 3 shells.—PS IX/3, sta. 220, 006°E, 118–126 m, 2 specimens (all in SMNH).

Distribution: Antarctic circumpolar in 36–765 m.

Redescription: We only describe the anatomy, based on three decalcified specimens of 2.5 mm diameter, and serial sections of three adult and two young males, two adult females, and one female pallial skirt. Shell, Figure 10A–C; protoconch, Figure 34F, G.

External morphology of soft parts: The head-foot and pallial complex comprises $\frac{2}{3}$ of a whorl in contracted specimens, the visceral mass slightly more than two whorls. The anterior part of the head-foot has a weak and diffuse granular grayish pigmentation, best visible along the edges of the snout, foot, and tentacles; behind the tentacles, including the visceral mass, it is light beige (in alcohol). The anterior $\frac{1}{10}$ whorl of the visceral mass is still paler because of the overlying kidney. At the left side, the pericardium with the ventricle and auricle lies directly behind the gill and osphradium. The gonad is not easily distinguished externally, even in sexually mature specimens. Directly behind the pericardium, the esophagus and stomach extend about a third of a whorl backward before the esophagus enters the rear part of the stomach. Forming a continuation of the anteriorly situated part of the stomach, the intestine very soon turns sharply to the right and disappears under the kidney.

The pallial cavity is quite deep, and the pallial skirt normally covers the whole head in preserved specimens. The pallial margin is thin and simple, without tentacles and papillae, except at the right $\frac{1}{2}$, where it is “uneven,” but the details could not be worked out. The osphradium

is surrounded by two ridges and runs along the gill from its most posterior part, forward to the anterior $\frac{1}{4}$ of the gill. The gill consists of a series of about 12 triangular leaflets, drawn out to a ventral tip; the gill width corresponds to $\frac{1}{4}$ of the pallial cavity. The leaflets in its central part are about twice as wide and high as the anterior ones. The columellar muscle projects at the right side of the body, 80–100° from the operculum. Its left part is much less conspicuous and narrower than the right. The hypobranchial gland is rather inconspicuous and partly covered by the tips of the gill leaflets. The pallial oviduct is restricted to the posterior right half of the cavity, and its left side contains the rectum, which opens at the same level as the duct. In the male, the rectum parallels the sperm duct and prostate in the corresponding position.

The head is medium-sized and has a pair of short (contracted), conical, flattened tentacles with large, black eyes in basal-lateral bulges. The snout is rather short, with parallel sides, somewhat flattened with a subventral mouth.

The male has a simple, tapering, finger-shaped penis just below the right cephalic tentacle, with a dorsal furrow containing a closed sperm duct. The duct continues buried in the right corner of the pallial cavity where there is a rather voluminous prostate.

The foot is flat, large, and broad. Judging from the folds, its anterior edge is probably blunt, but the corners seem not to be drawn out to small, tentaclelike extensions. Posteriorly, it seems bluntly rounded. There is no distinct opening for the posterior pedal gland; anteriorly, between the distinctly set-off propodium and the mesopodium opens an anterior pedal gland. The sides of the foot are smooth, and there are no epipodial ridges or furrows.

Internal anatomy (Figure 12): The foot is almost filled by the large posterior pedal gland (Figure 12A, **ppg**). The slightly smaller anterior pedal gland bulges into the cephalopodal haemocoel, but not behind the nerve ring. The posterior pedal gland stains dark bluish violet, the anterior one, a much lighter grayish violet with conspicuous nuclei. The posterior pedal gland does not have a defined opening. The anterior one has a storage space under the propodium lined with tall epithelium and opens via a broad and flat duct, which penetrates most of the gland. The muscle layer of the foot is quite thin (height 75–100 μ m) along the sides and ventrally.

The tentacles are solid and muscular all the way to the base where they have a subcutaneous eye with lens and pigment layer, in a bulge. The snout is very muscular and

Explanation of Figure 12

Trilirata macmurdensis, two sagittal sections. Figure A. Oblique longitudinal section through left part of head-foot. Figure B. Oblique longitudinal section through right part of head-foot. **aa**—anterior aorta; **apg**—anterior pedal gland; **cg**—(right and left respectively) cerebral ganglion; **cm**—columellar muscle; **ct**—cephalic tentacle; **g**—tips of gill leaflets (embedded in mucus); **hg**—hypobranchial gland; **k**—kidney; **oeg**—esophageal gland; **pe**—penis; **pg**—pedal ganglion; **plg**—pleural ganglion; **rc**—radular cartilage; **re**—bulges from rectum; **rs**—radular sac; **s**—statocyst; **sd**—seminal duct; **sg**—salivary gland; **sn**—snout. Scale lines = 200 μ m.

can probably be extended considerably when the snail is grazing.

The alimentary system consists of the mouth; a large, rather muscular buccal mass; a very short anterior esophagus; a large esophageal gland; a narrow posterior esophagus; stomach; intestine; and rectum. From the posterior esophagus backward, the preservation was too poor for any detail other than that the stomach has a gastric shield but seems to lack a crystalline style.

The jaw is reduced to a thick cuticular lining of the oral tube.

The radular sac is straight, long, and slender, passes backward through the nerve ring and lies ventral to the esophageal gland, extending as far back as this where it curves dorsally to the right of the esophagus. The part of the radula in use is supported by a pair of large cartilages.

Two salivary glands (Figure 12A, B, **sg**) open into the buccal cavity close to its mid-line via short, inconspicuous ducts, which do not pass through the nerve ring. The salivary glands are large and situated in front of and above the cerebral ganglia. Each consists of a short, thin duct and a voluminous gland of several lobes. With EHE they stain violet.

The dorsal food channel is characterized by the rich occurrence of mucus-producing cells. These start in the posterior, dorsal part of the buccal cavity, get displaced toward the left side when passing the nerve ring and end up ventrally in the esophageal gland (Figure 12A, **oeg**) where they do not reach its posterior end. No structure which could be a pair of esophageal pouches was found. Most specimens had foraminiferans in various stages of digestion in the stomach, intestine, and rectum. In the rectum these consist of almost empty "husks" containing some particles, which stain blackish violet with EHE.

The nervous system follows the normal pattern of littorinids with dialyneurys between the left pleural and the supraesophageal ganglia. The distances between the ganglia are fairly short (contracted specimen), the pleural and cerebral ganglia abutting. The supra- and subesophageal ganglia are situated less than twice their diameter from the corresponding pleural ganglion. The length of the connectives to the pedal ganglia are twice the diameter of these ganglia. The supraesophageal ganglion lies free at the left side of the cephalopedal haemocoel; the subesophageal one in a pit in the body wall. The buccal ganglia are situated dorsally on the buccal mass close to the exit of the esophagus, and connected by a commissure. In front of the pedal ganglia is an accessory pedal ganglion, connected by a connective of the same length as its own diameter and innervating the anterior pedal gland and propodial area.

The statocysts are situated above and behind the pedal ganglia and are slightly displaced laterally. Their diameter corresponds to half the length of the ganglion. They have a single statolith.

Reproductive system. The sexes are separate. The fixation does not, however, allow any detailed description of

the systems. The gonad lies along the right side of the visceral mass.

Female. An ovarian duct leads to a large albumen gland, which stains very lightly. Along the left side and anterior half of the albumen gland is a capsule gland (staining dark violet with EHE), but the detailed morphology and connections of these could not be worked out due to histolysis and missing and ruptured sections. They are, however, closed except for a short opening close to the anterior end of the capsule gland, and there is no bursa copulatrix. Just behind the capsule gland and above the albumen gland is a receptaculum seminis, which opens to the connection between the capsule and albumen gland. It contains oriented sperm. A well-developed gonopericardial duct is present, opening into the ovarian duct close to the albumen gland. Four of the five females that were sectioned had the pericardium filled with sperm.

Male. The simple, tapering penis is situated below the right cephalic tentacle. It has a seemingly open sperm groove along its dorsal side, but this furrow contains a closed sperm duct, which turns to the right side and runs backward in the right corner of the pallial cavity. Along the most posterior part in the cavity lies a closed prostate gland, which continues backward abutting the rectum and the kidney, and eventually extends into the visceral mass at the right side of the kidney. The epithelium of the prostate is divided into the more dorsal half, which is covered by tall cylindrical epithelium, staining violet with EHE, and the more ventral half, covered by much less ordered cells of an almost cotton or wool-like structure, which stains bluish gray with EHE. The vas deferens seems to open into the prostate at its anterior $\frac{1}{3}$. The more posterior part of the vas deferens lies coiled close to the columella, is voluminous, thin-walled, and functions for storage of sperm.

The radula (Figures 6C-F, 11A-C) is taenioglossate, long, and slender, with about 100 transverse rows of teeth. The central tooth (Figures 6D, 11A) has a low and indistinct hood with a few tubercles along its apical margin. Below this, one large central and one smaller cusp on each side form a cutting edge. Beside these, and partly concealed by them, are two much smaller denticles on each side. The "wings" are not drawn out to small denticles on the sides. The front of the tooth is concave and lacks a supporting bulge at the base. The lateral tooth usually has six denticles, of which numbers 1 and 3 (counted from the inner edge) are at least twice the size of the others. The littorinid notch is missing. The first marginal tooth is simple, claw-shaped, slightly flattened with a sturdy shaft and three large apical cusps. The outer marginal tooth is longer and a fourth the thickness of the inner one. It has three long and slender apical cusps. At mid-length, the shaft is crossed by a furrow and has a small, very thin, and membranous cusp (Figure 11C). This furrow makes the tooth pliable, and the outer part is frequently folded here (Figures 6E, 11B). Very young specimens have a proportionally shorter

radula with fewer transverse rows of teeth, otherwise identical (Figure 6C).

The operculum (Figure 4I) has a few whorls and central nucleus, is transparent, slightly yellowish brown, especially where it is attached to the foot. The surface is distinctly wrinkled by the growth lines.

Reproduction. The eggs are laid singly in simple, globular capsules with a thin, transparent wall. The size of the young in capsules agrees with our smallest benthic stages, and the development is thus lecithotrophic and encapsulated.

Remarks: Powell (1958:191) suggested that *Prolacuna trilirata* is a synonym of *P. macmurdensis*. This was accepted by Arnaud (1972:126) and Dell (1990:163), and we can see no reason to question this, although there is considerable variation in the shell morphology (Figure 10A–C).

Trilirata herosae Warén & Hain, sp. nov.

(Figures 4J, 11D, E, 13E–H)

Type locality: BIOCAL DW35, New Caledonia, 23°10'S, 167°10'E, 675–680 m.

Type material: Holotype and 2 paratypes (from DW70) in MNHN.

Material examined: BIOCAL sta. DW70, New Caledonia, 23°25'S, 167°53'E, 965 m, 2 shells (paratypes), MNHN.—BIOCAL sta. DW46, New Caledonia, 22°53'S, 167°17'E, 570–610 m, 2 shells.

Distribution: Only known from the material examined, from south of New Caledonia, in 570–965 m.

Etymology: “*herosae*,” after Mme. Virginie Heros, MNHN, who has sorted a large part of the sediments in which the species was found.

Description: *Shell* (Figure 13E–G) angular, low-spined, with three spiral keels and a wide umbilicus. The protoconch (Figure 13H) is not demarcated, is sculptured with some spiral ribs and keels and some indistinct bumps and dents. The proto- and teleoconch together form 2.5 whorls, sculptured by indistinct and irregular growth lines, some indistinct and low spiral striae, and three strong spiral keels, one at the edge of the shoulder, one at the periphery, and one around the umbilicus. The umbilicus is deep, penetrating shell to the protoconch, and of a diameter corresponding to 45% of the shell diameter. The parietal callus is thin. The inner lip is evenly curved, the outer lip almost straight between the suture, the spiral keels, and the lower corner of the aperture.

Dimensions. Diameter of holotype (largest specimen) 3.7 mm.

The radula (Figure 11D, E) is taenioglossate, long, and slender with about 80 transverse rows of teeth. The central tooth has a low, thin hood with no cusps. Below this, one

major central and three smaller, lateral, rounded cusps form a cutting edge. The “wings” are not drawn out to small denticles. The front of the tooth is deeply excavated. The lateral tooth usually has about 10 denticles, of which numbers 1 and 3 (counted from the inner edge) are at least twice the size of the others. The littorinid notch is missing. The first marginal tooth is simple, claw-shaped, with a sturdy shaft and eight apical cusps. The apical four of these cusps are very long; the more basal four are situated along the outer edge and are less than half the size of the others. The outer marginal tooth is of about the same length, much thinner, with four long apical digits of $\frac{1}{2}$ the length of the tooth. At mid-length, the shaft has a transverse groove where it is much thinner and equipped with a very thin, triangular cusp (Figure 11E).

The operculum (Figure 4J) has a few whorls, a distinctly subcentral nucleus, and is transparent, pale brownish yellow, more distinctly so where attached to the foot. The surface is distinctly wrinkled by the growth lines.

Remarks: The shell has some resemblance to that of *Aorotrema* Pilsbry & McGinty, 1942 (now in Vitrinellidae: Abbott, 1974). Species of that genus, however, have a rough surface, a columellar tooth, and a hyperstrophic larval shell. Their closer affinity remains unknown, since only empty shells are known, but the Pyramidellidae is probably a good guess.

Trilirata triregis Warén & Hain, sp. nov.

(Figure 13A–D)

Type locality: Northern New Zealand, off Three Kings Islands, 34°00'S, 171°51'E, 800 m.

Type material: Holotype and 14 paratypes, MNZ M.49033 and 127384.

Material examined: Northwestern New Zealand, northwest of Three Kings Islands, Middlesex Bank, 34°02.0'S, 171°44.0'E, 246–291 m, 3 shells, MNZ M.118932.—Three Kings Islands, 24 km northwest of Great Island, 34°05.9'S, 171°55.1'E, 710 m, 9 shells, MNZ M.118934.—Three Kings Islands, 11 km northwest of Great Island, 34°06.5'S, 172°04.7'E, 310 m, 1 shell MNZ M.118931.—Three Kings Islands, 18 km north of Great Island, 33°59.2'S, 172°13.6'E, 155 m, 1 shell, MNZ M.118929.—Three Kings Islands, 13 km north of Great Island, 34°01.8'S, 172°12.0'E, 508 m, 1 shell, MNZ M.118928.—Northwest of Three Kings Islands, Middlesex Bank, 34°00.9'S, 171°44.7'E, 201–216 m, 1 shell, MNZ M.118935.

Distribution: Only known from the material examined from the Three Kings Islands area, 155–800 m (shells only).

Etymology: “*triregis*” (Latin) from *tri* and *rex*, meaning “of the three kings,” referring to the type locality.



Explanation of Figure 13

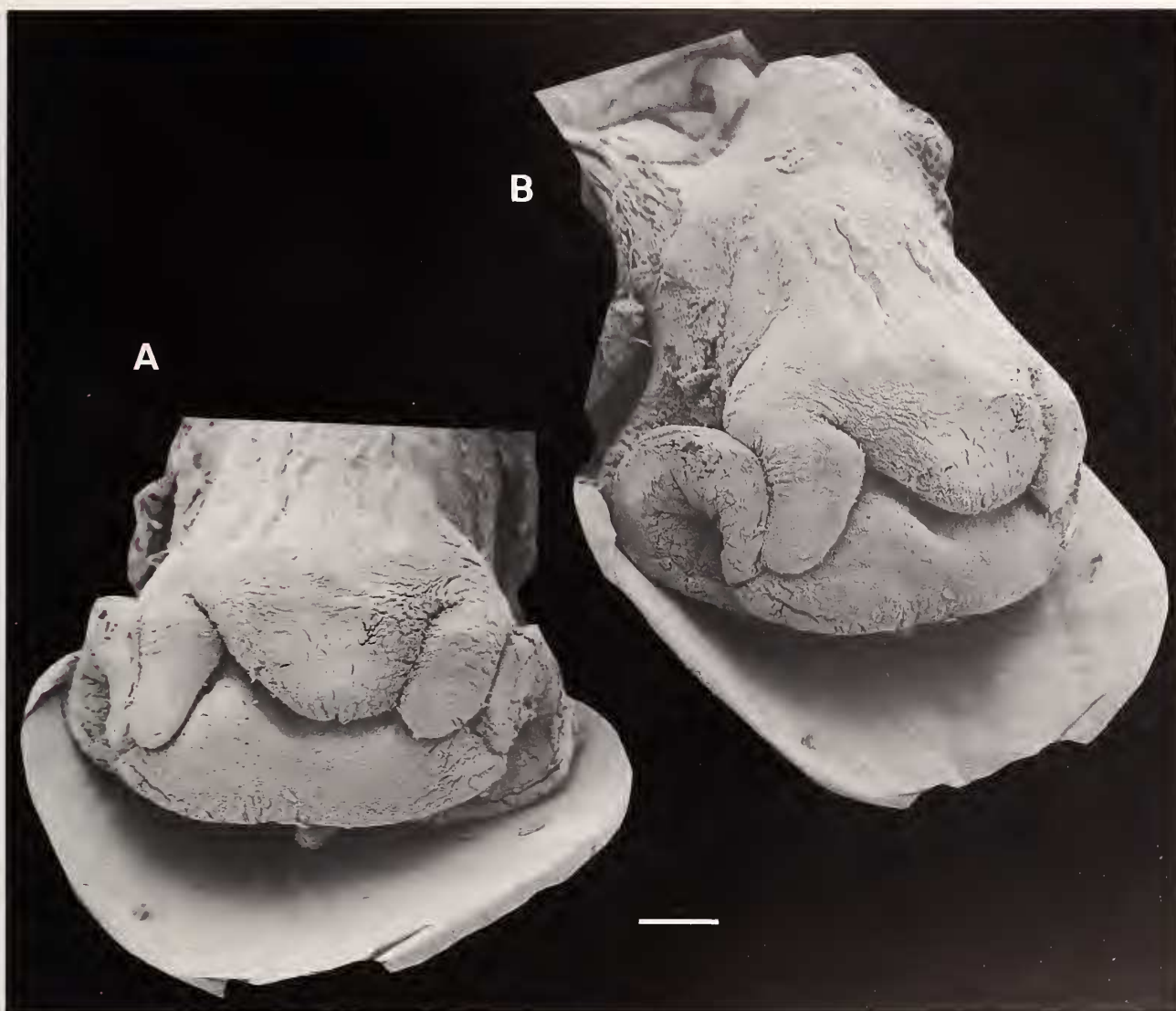
Trilirata spp. Figure A. *T. triregis* Warén & Hain, sp. nov. Holotype, diameter 2.8 mm. Figures B-D. *T. triregis* Warén & Hain, sp. nov. Paratypes, diameter 1.3, and 2.25 mm. Figure E, F. *T. herosae* Warén & Hain, sp. nov. Holotype, diameter 3.7 mm. Figures G, H. *T. herosae* Warén & Hain, sp. nov. Paratype, diameter 3.2 mm. Scale lines = 200 μ m.

Description: *Shell* (Figure 13A, B, D, E) angular, low-spired, with three spiral keels and a wide umbilicus. The protoconch (Figure 13C) is not demarcated and almost smooth. The proto- and teleoconch together form about 2.6 whorls, sculptured by indistinct and irregular growth lines, and three strong spiral keels, one at the edge of the shoulder, one at the periphery, and one around the umbilicus. The umbilicus is deep, penetrating the shell to the protoconch, and of a diameter corresponding to 45% of the

shell diameter. The parietal callus is thin. The inner lip is evenly curved, the outer lip almost straight between the suture, the spiral keels, and the lower corner of the aperture.

Dimensions. Diameter of holotype (largest specimen) 2.8 mm, height 2.8 mm.

Remarks: *Trilirata triregis* resembles *T. herosae*, and close relations between the two seem beyond doubt, despite



Explanation of Figure 14

Trilirata sexcarinata Warén & Hain, sp. nov., PS VII/4, sta. 291. Figure A. Front view of head-foot. Figure B. Slightly oblique view of right side of the foot. Scale line = 200 μ m.

no soft parts being available of *T. triregis*. The only noticeable difference is that *T. herosae* is slightly larger at the same number of whorls and has a more pronounced spiral sculpture on the basal surface.

The holotype of *T. triregis* is the largest specimen available, but its aperture is broken. Also, the smaller specimens are in rather bad condition, and it is possible that the specimens are fossil.

Trilirata sexcarinata Warén & Hain, sp. nov.

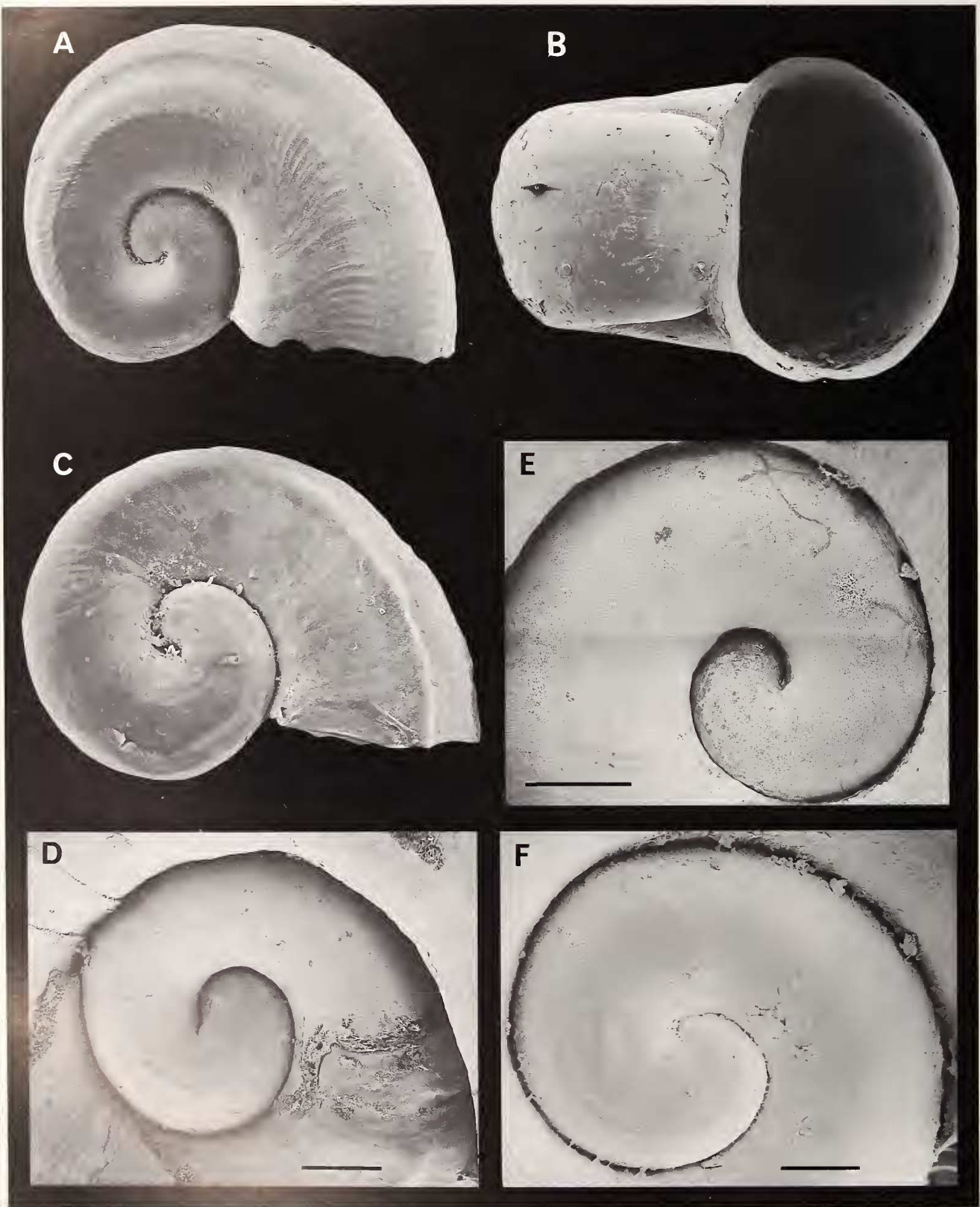
(Figures 4K, L, 11F, G, 14, 15A, B, 16–18)

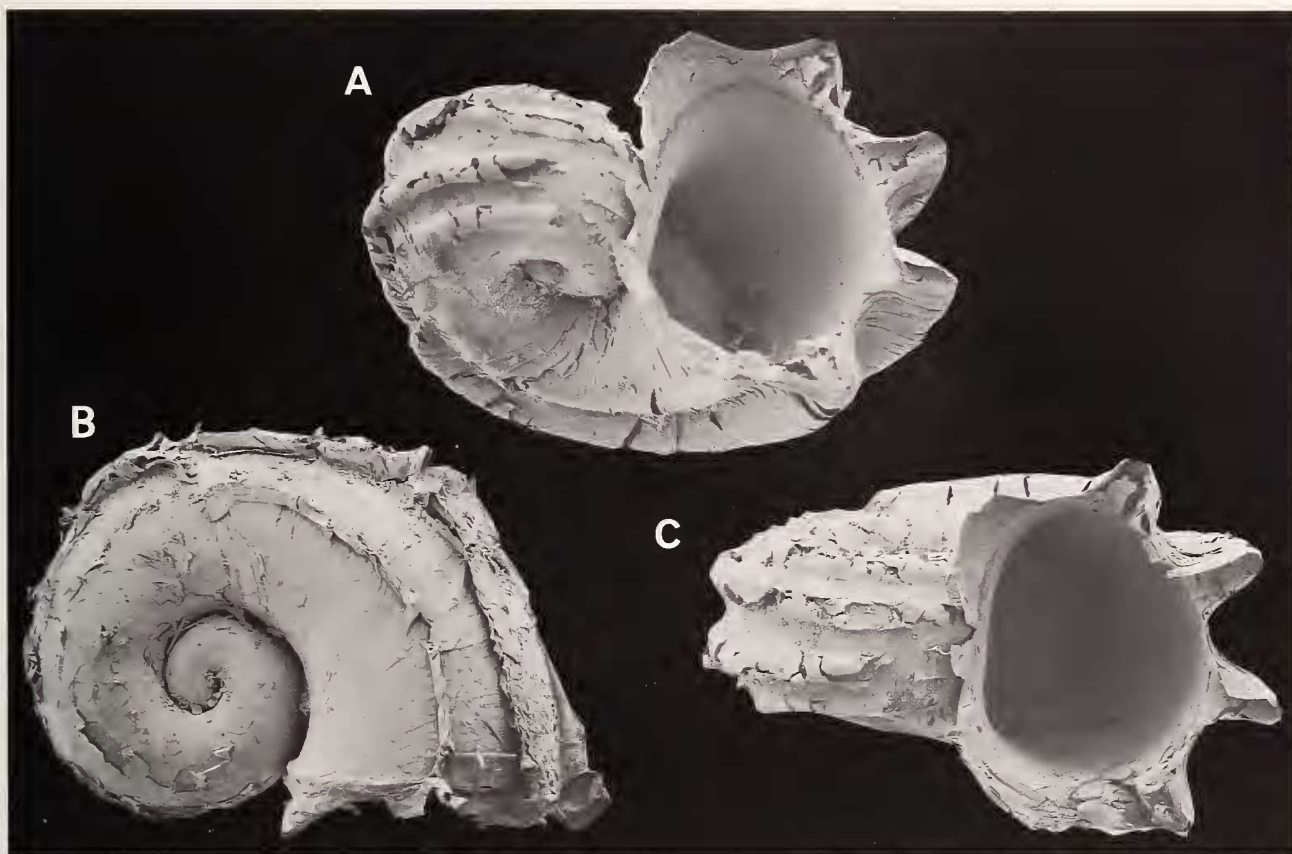
Mesogastropoda sp. 1: Hain, 1990:53, pl. 3, fig. 7a–f; pl. 22; fig. 5.

Type locality: PS IX/3, sta. 220, 70°24.1'S, 06°07.6'E–70°24.3'S, 06°08.6'E, 118–126 m, 13 March 1991.

Type material: Holotype and 4 paratypes (immature, from sta. 179) in SMNH, nos. 4658 and 4659.

Material examined: PS VII/4 sta. 284, 013°W, 402–412 m, 2 specimens.—PS VII/4 sta. 291, 012°W, 499–515 m, 1 specimen.—PS VII/4 sta. 293, 012°W, 771–793 m, 1 specimen.—PS IX/3, sta. 165, 003°W, 191–204 m, 1 specimen, 1 shell.—PS IX/3, sta. 173, 007°E, 739–765 m, 2 specimens, 3 shells.—PS IX/3, sta. 179, 007°E, 185–161 m, 1 specimen, 6 shells.—PS IX/3, sta. 180, 006°E, 280–298 m, 1 specimen.—PS IX/3, sta. 212, 003°E, 568–644





Explanation of Figure 16

Trilirata sexcarinata Warén & Hain, sp. nov., PS VII/4, sta. 284. Figures A–C. Diameter 2.5 and (B) 2.1 mm.

m, 1 shell.—PS IX/3, sta. 220, 006°E, 118–126 m, 2 specimens (all in SMNH).

Distribution: Weddell and Lazarev seas, from 13°W, eastward to 7°E, in 118–765 m.

Etymology: “*sexcarinata*” (Latin), with six keels.

Description: Based on the material above; three adult sectioned females, one critical point dried female, and two decalcified males.

Shell (Figure 16) large for the genus, corneous, planispiral with strongly convex whorls and strong spiral keels. The protoconch (Figure 15A) is poorly demarcated, smooth, consists of about 1 whorl of a diameter of 0.6 mm.

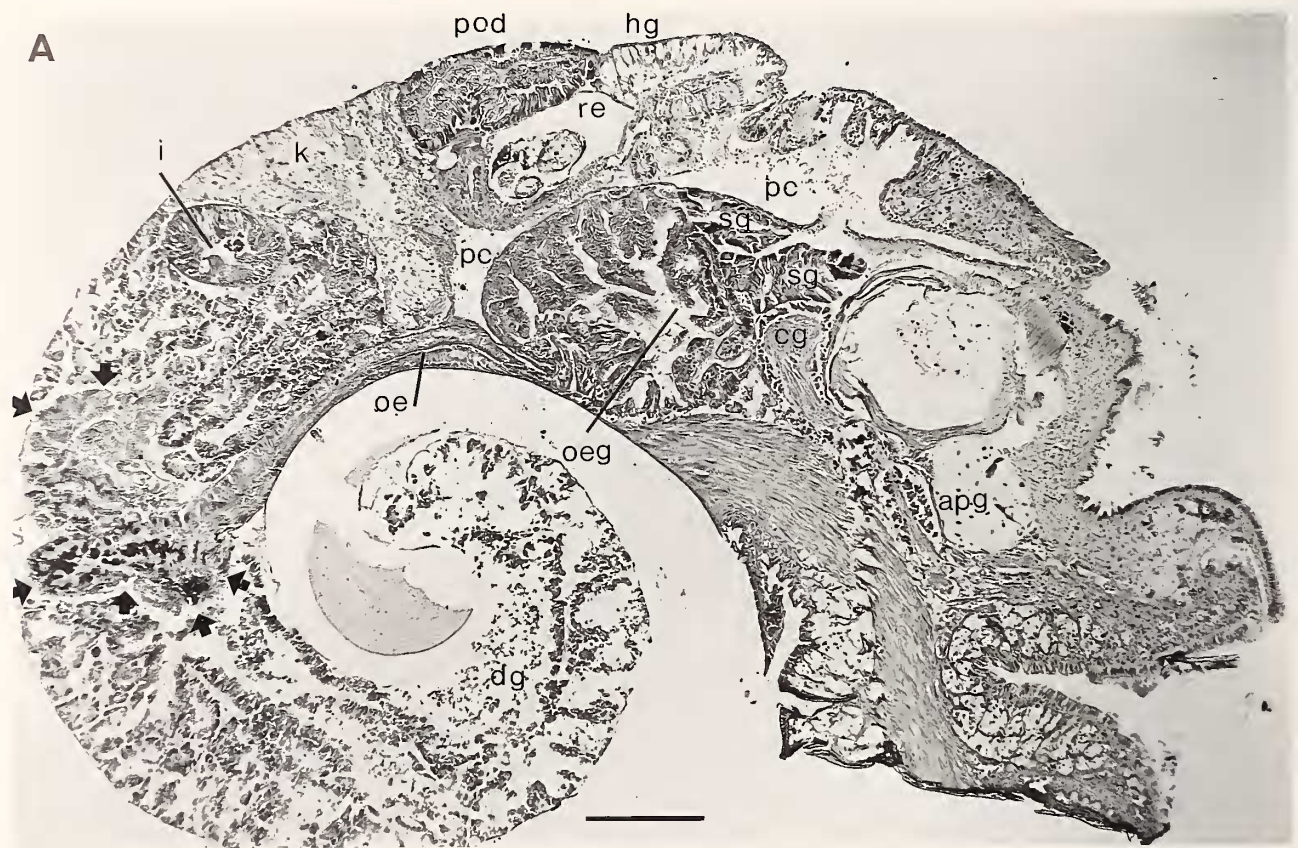
Adult specimens have 2 teleoconch whorls, sculptured by uniform and distinct incremental lines. The spiral sculpture of the teleoconch starts with three spiral ribs which rapidly fade away. The aperture is higher than broad, evenly rounded, not indented by the preceding whorl. The periostracum is extremely thick, and forms six spiral keels, one keel at the most apical part of the shell, one at the basal part of shell, and four keels between these.

Dimensions. Holotype 2.6 mm, maximum diameter 6 mm.

External morphology of soft parts: The head-foot (Figure 14) and pallial complex comprise $\frac{1}{4}$ of a whorl in a contracted specimen, the visceral mass 1.5–2 whorls. The

Explanation of Figure 15

Figures A, B. *Trilirata sexcarinata* Warén & Hain, sp. nov., young specimens, PS IX/3 sta. 179, diameter 1.33 and 1.17 mm. Figures C–E. *Zerotula stellapolaris* Warén & Hain, sp. nov., PS IX/3 sta. 179, diameter 0.45 mm. Figure F. *Zerotula incognita* Warén & Hain, sp. nov., holotype. Scale lines = 100 μ m.



head-foot is pale beige. The visceral mass is brownish or greenish (in alcohol), its anterior $\frac{1}{10}$ whorl is paler and contains the kidney and most of the albumen gland of the oviduct. At the left side, the pericardium with the ventricle and auricle lies directly behind the gill and osphradium, in females strongly iridescent from its contents of sperm. The gonad is not easily distinguished externally, although the specimens are sexually mature. The esophagus and stomach cannot be discerned externally.

The columellar muscle is inconspicuous and projects at the right and left side of the body, 70–90° from the operculum; dorsally it reaches less than $\frac{1}{2}$ of the height of the whorl and is thus mainly ventral. Its left part is far less conspicuous and narrower.

The pallial cavity is quite deep, and the pallial skirt normally covers the whole head in preserved specimens. The pallial margin is thin and simple, without tentacles or papillae. The osphradium is encircled by two ridges and runs along the gill from its most posterior part, forward to the anterior $\frac{1}{4}$ of the gill. The gill consists of a series of about nine triangular leaflets, drawn out to a ventral tip; the gill width corresponds to $\frac{1}{4}$ of the pallial cavity. The leaflets in its central part are about twice as wide and high as the anterior ones. The hypobranchial gland is rather inconspicuous and partly covered by the tips of the gill leaflets. The brown pallial oviduct is restricted to the posterior right half of the cavity, and its left side contains the rectum, which opens at the same level as the duct.

The head is medium-sized and has a pair of short (contracted), conical, flattened tentacles with large, black eyes in basal-lateral bulges. The snout is rather short, slightly tapering, somewhat flattened with a subventral mouth.

The foot is flat, large, and broad. It is strongly contracted in all specimens, but judging from the folds, its anterior edge is probably blunt. Posteriorly it seems bluntly rounded. Anteriorly, between the indistinctly set-off propodium and the mesopodium opens an anterior pedal gland. The sides of the foot are smooth and there are no epipodial ridges or furrows.

Internal anatomy (Figures 17, 18): The foot (Figure 18A) is almost filled by the large posterior pedal gland (ppg) and the slightly smaller anterior pedal gland (apg). These do not bulge into the cephalopedal haemocoel. The posterior pedal gland stains dark bluish violet, the anterior one, a much lighter grayish violet. The posterior pedal

gland has no defined opening. The anterior one has a storage space under the propodium lined with tall epithelium and opens via the slit between the pro- and mesopodium. The muscle layer of the foot, 75–100 μm thick along the sides and ventrally, is rich in muscle fibers.

The tentacles are solid and muscular all the way to the base where they have a subcutaneous eye with lens and pigment layer, in a bulge. The snout is very muscular and can probably be extended considerably when the snail is grazing.

The alimentary system consists of the mouth, a large, not very muscular buccal mass, a very short anterior esophagus, a large esophageal gland, a narrow posterior esophagus, a poorly defined stomach, intestine, and rectum.

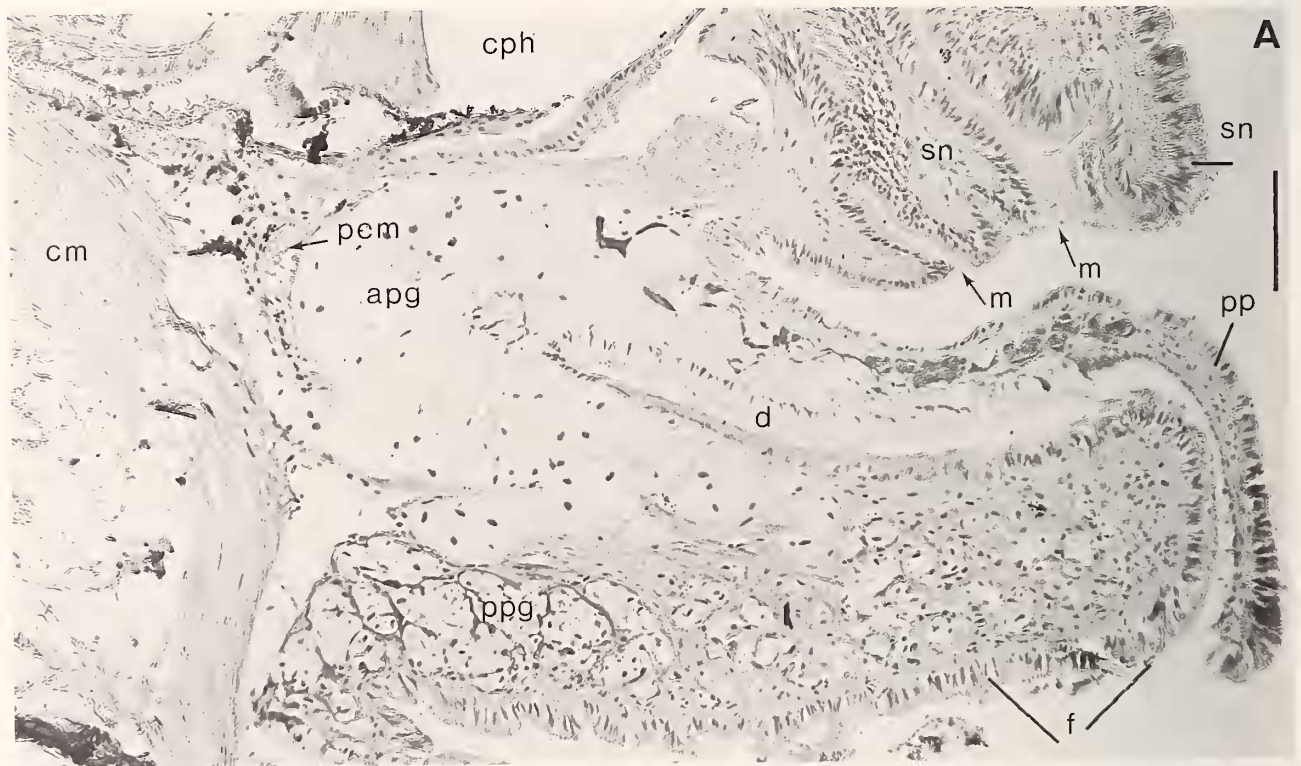
The jaw is thin and membranous, only a thick cuticle lining of the oral tube.

The radular sac (Figure 18B, rs) is straight, long, and slender, passes backward through the nerve ring below the esophageal gland and extends as far back as this. The part of the radula in use is supported by a pair of large cartilages.

Two salivary glands (Figure 18, sg) open into the buccal cavity close to its mid-line via short, inconspicuous ducts which do not pass through the nerve ring. The salivary glands are large and situated above the cerebral ganglia. Each consists of a short, thin duct and a longer, coiled glandular tube. The shallow dorsal food channel is characterized by the rich occurrence of mucus-producing cells. These start in the posterior, dorsal part of the buccal cavity, get displaced toward the left side when passing the nerve ring and end up ventrally in the esophageal gland where they do not reach its posterior end. A pair of esophageal pouches seems to be present, but this is uncertain. The interior of the esophageal gland (Figure 18B) is filled by glandular, transverse septa which leave only a small ventral lumen for the (now ventral) dorsal food channel. The posterior esophagus exits from the gland as a much narrower, internally strongly ciliated tube of $\frac{1}{2}$ of the diameter of the gland. It continues backward where it ends in a large cavity formed by the digestive gland. From this cavity a very simple stomach, without gastric shield, continues and goes over into the intestine, which is twice the diameter of the stomach. The intestine continues with a thick wall, turns to the right just behind the kidney, crosses the body, turns abruptly forward ventrally to the kidney. It continues forward surrounded by the lobes of the albumen gland

Explanation of Figure 17

Trilirata sexcarinata Warén & Hain, sp. nov. Figure A. Longitudinal section, left side of body. Stomach (histolysed) demarcated by a series of black arrows. Figure B. Longitudinal section, right side of body. apg—anterior pedal gland; cg—cerebral ganglion; cm—columellar muscle; dg—digestive gland; hg—hypobranchial gland (distorted and jammed with part of gill); i—intestine; od—oviduct; oe—esophagus; oeg—esophageal gland; ov—ovary; pc—pallial cavity; pg—pedal ganglion; plg—pleural ganglion; pod—pallial oviduct; re—rectum (with remains of forams); s—statocyst; sg—salivary gland. Scale lines = 250 μm .



and goes over into a much more thin-walled rectum when it enters the pallial skirt. Most specimens had remains or almost complete forams in the digestive canal.

The nervous system follows the normal pattern, with dialyneury between the left pleural and the supraesophageal ganglia. The distances between the ganglia are fairly short (contracted specimen), the left pleural and cerebral ganglia partly fused, the right ones abutting. The supra- and subesophageal ganglia are situated less than their diameter from the corresponding pleural ganglion. The length of the connectives to the pedal ganglia is twice the diameter of the ganglia. The supraesophageal ganglion lies free in the left side of the cephalopedal haemocoel beside the left cerebral ganglion; the subesophageal one is well embedded in the body wall slightly farther back. The buccal ganglia are situated dorsally on the buccal mass close to the exit of the esophagus, and connected by a commissure. In front of the pedal ganglia is an accessory pedal ganglion connected by a connective of its own length and innervating the anterior pedal gland and propodial area.

The visceral ganglia were not identified.

The statocysts (with a single statolith) are situated above and behind the pedal ganglia and slightly displaced to the right. Their diameter corresponds to the width of the ganglion.

Reproductive system. The sexes are separate, or at least the three sectioned specimens were females with no trace of male organs. The fixation does not, however, allow any detailed description. The ovary lies along the right side of the visceral mass. An inconspicuous ovarian duct close to the ventral body wall leads to a large albumen gland, which stains very lightly. Along the left and anterior side of this is a capsule gland (staining dark violet). The pallial oviduct system bulges deep into the visceral mass, occupying about 80° of the whorl and extending from the ventral to the dorsal edge of the body. The detailed morphology could not be worked out due to missing sections. There is no receptaculum seminis, but oriented sperm is stored in the pericardium (which communicates with the oviduct via the gonopericardial duct).

The radula (Figure 11F, G) is taenioglossate, long, and slender with about 80 transverse rows of teeth. The central tooth has a low and thin, slightly undulating hood with a triangular cusp at each end along its apical margin. Below this, one major central and two smaller, lateral, rounded cusps form a cutting edge. Beside these and partly concealed by them is a much smaller denticle on each side.

The "wings" are drawn out to a small denticle on each side close to the base. The front of the tooth is deeply excavated. The lateral tooth usually has about seven denticles, of which number 4 (counted from the inner edge) is at least twice the size of the others. The littorinid notch is missing. The first marginal tooth is simple, claw-shaped, with a sturdy shaft and six apical cusps. The inner three of these cusps are very long, the outermost one is a mere denticle. The outer marginal tooth (Figure 11F) is of about the same length, much thinner, with three long apical digits of $\frac{1}{2}$ the length of the tooth. Halfway to the point, the shaft has a transverse groove where it is much thinner and equipped with a very thin and triangular cusp.

The operculum (Figure 4K, L) has a few whorls, distinctly subcentral nucleus; it is transparent, slightly brownish yellow, especially where it is attached to the foot. The surface is distinctly wrinkled by the growth lines.

Remarks: The shell of this species bears some resemblance to echinospira larvae in that the periostracum to a large extent is separated from the shell by a transparent, gelatinous layer which dries to virtually nothing. It also resembles closely an unidentified gastropod larva figured by Pelseneer (1903:figs. 61–63), but that larva has a different type of radula and velar lobes, and seems to belong to a capulid, possibly a species of *Torellia*, judging from the radula.

It may seem strange to classify *T. sexcarinata* with a very strongly developed periostracum in the same genus as *macmurdensis* and *herosae*, which have a very thin periostracum. Such differences in periostracal structure are, however, also known in the genus *Lacuna*, where *L. vineta* has a normal periostracum and *L. crassior* (Montagu, 1803) has a very thick periostracum, which dries to a thin skin (A. Warén, unpublished).

Trilirata sexcarinata looks very different from the other species of *Trilirata*, especially in alcohol when the periostracum is intact. However, when the initial part of a cleaned teleoconch is compared, they are much more similar (Figures 15A and 34G). The radulae are virtually identical, especially the extra cusp halfway along the shaft of the outer marginal, and we consider these good synapomorphies for bringing the species together in a distinct genus.

Young specimens (Figure 15A, B) have a proportionally broader shell than *Zerotula stellapolaris* and lack the hypertrophied periostracum.

Explanation of Figure 18

Trilirata sexcarinata Warén & Hain, sp. nov. Figure A. Longitudinal section through center of anterior part of foot and snout. Figure B. Longitudinal section through central part of head-foot. **apg**—anterior pedal gland; **cc**—cerebral commissure (embedded in anterior esophagus and esophageal gland); **cm**—columellar muscle; **cph**—cephalopedal haemocoel; **d**—duct from apg; **f**—foot (mesopodium); **g**—gill leaflets; **m**—mouth (between arrows); **pcm**—pedal commissure; **pp**—propodium; **ppg**—posterior pedal gland; **ps**—pallial skirt; **r**—radula; **rc**—radular cartilage; **re**—rectum; **rs**—radular sac; **sg**—salivary gland; **sn**—snout. Scale lines = 100 μ m.

Zerotula Finlay, 1926

Zerotula Finlay, 1926:379. Type species *Discohelix hedleyi* Mestayer, 1916 by original designation.

Remarks: *Zerotula* was included in Architectonicidae by Finlay (1926). It has later been used almost exclusively by Powell (1979 and other references), who has kept it in the Architectonicidae without comments. Several of the species classified in *Zerotula* by Powell are here referred to other genera.

The shells of the species here included in *Zerotula* vary considerably in sculpture, but the three (four?) species of which we know the radula have a very uniform lateral tooth, which is remarkably broad and low. *Zerotula incognita* resembles the species of *Trilirata* in having an outer marginal tooth with a thinner zone with a cusp (Figure 22A; cf. *T. macmurdensis*, Figure 11C), which convincingly shows the genera to be related, since no similar structure is known in any other gastropod group.

We have searched museum collections and the literature for species which have been placed in the wrong genera or families, but so far there are no candidates for inclusion in *Zerotula*, except the species included below.

For the systematics of *Discohelix* (Archaeogastropoda) where *Zerotula hedleyi* originally was classified, see Warén, Gofas, & Ponder (in preparation).

Zerotula hedleyi (Mestayer, 1916)

(Figures 3A, B, 4A, 19A–C, 20F)

Discohelix hedleyi Mestayer, 1916:125, pl. 12, figs. 6–6b.
Zerotula hedleyi: Finlay, 1926:379.

Type locality: New Zealand, Three Kings Islands, 15°S of Big King, 175 m depth.

Type material: Holotype and one paratype in MNZ, one paratype in AMS, not examined.

Material examined: New Zealand. Off Three Kings Islands, 34°11'S, 172°10'E, 90 m, 14 shells, 5 specimens (dried), MNZ M.33660.—Off Three Kings Islands, 34°00'S, 171°55'E, 805 m, 2 shells, MNZ M.11847.—11 km northwest of Great Island, Three Kings Islands, 34°06.5'S, 172°04.7'E, 310 m, 30 shells, MNZ M.118153.—Middlesex Bank, Three Kings Islands, 33°59.8'S, 171°46.8'E, 143–163 m, 1 shell, MNZ M.118309.—Southeast of Great Island, Three Kings Islands, 34°14.1'S, 172°09.0'E, 192–202 m, 14 shells, MNZ M.118306.—Middlesex Bank, Three Kings Islands, 34°01.4'S, 171°45.2'E, 201–216 m, 1 shell, MNZ M.118308.—King Bank, northeast of Three Kings Islands, 33°57.4'S, 172°19.4'E, 128–123 m, 35 shells, MNZ M.118307.—Off Three Kings Islands, 34°10'S, 172°12'E, 250 m, 6 shells, MNZ M.34081.—Off Three Kings Islands, 34°00'S, 171°55'E, 805 m, 4 shells, MNZ M.118147.—Southeast of Great Island, Three Kings Islands, 34°14.8'S, 172°13.6'E, 173–178 m, 10 shells, MNZ

M.118150.—Southeast Bay, Great Island, Three Kings Islands, 54 m, 1 shell, MNZ M.33904.—North of Three Kings Islands, 34°01'S, 172°07'E, 700 m, 25 shells, MNZ M.34687.

Distribution: North of New Zealand, around Three Kings Islands; depth range 54–805 m (shells), found alive only once, in 90 m, MNZ M.33660.

Redescription: We have only described the radula and operculum; no soft parts are available. Shell, Figure 19A–C; protoconch, Figure 20F.

Radula. The radula (Figure 3A, B) is long and slender with close to 100 transverse rows of teeth. The central tooth is small and has a very low and indistinct hood. Below this, one major central and three smaller, lateral, rounded cusps form a cutting edge. The “wings” are not drawn out to small denticles at the sides. The front of the tooth is not excavated. The lateral tooth usually has about 10 denticles, of which number 1 (counted from the inner edge) is twice and number 3 is three times the size of the others. The six outer ones form a rather even “comb.” The littorinid notch is missing. The first marginal tooth is simple, claw-shaped, with a sturdy shaft and forked point (two or three cusps). The outer marginal tooth is the same length but much thinner and flatter, with two long apical digits of ½ the length of the tooth.

The operculum (Figure 4A) has a few whorls, an almost central nucleus, and is transparent. The surface is indistinctly wrinkled by the growth lines.

Remarks: *Zerotula hedleyi* (Figure 19A–C) resembles *Z. coronata*, sp. nov. (Figure 19D–F), but lacks the tubercles on the spiral keels.

Zerotula coronata Warén & Hain, sp. nov.

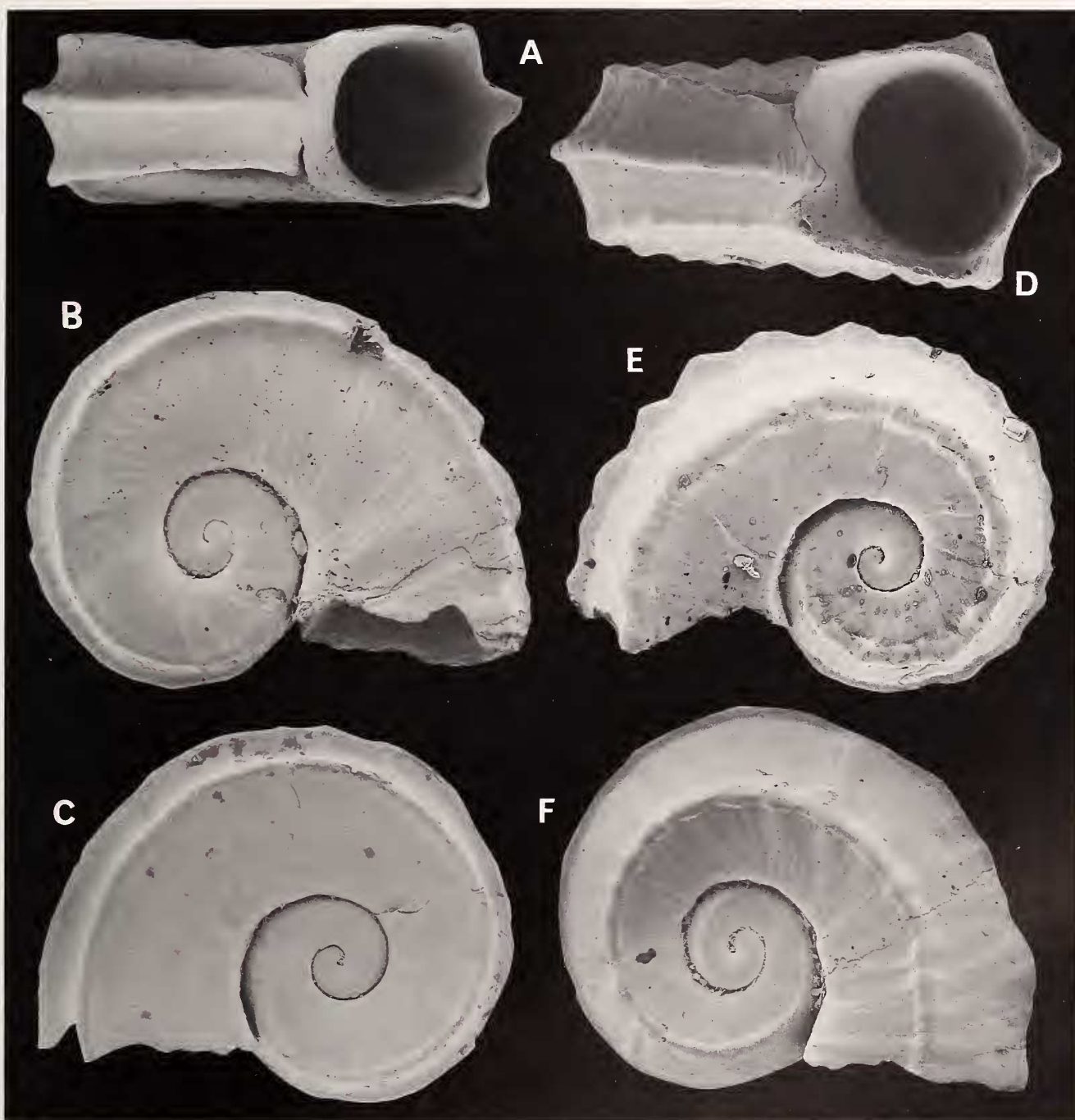
(Figures 19D–F, 20E)

Type locality: Off Three Kings Islands, 34°00'S, 171°55'E, 805 m, 40 shells.

Type material: Holo- and 39 paratypes MNZ, nos. M.49224 and 118852.

Material examined: New Zealand, Middlesex Bank, northwest of Three Kings Islands, 34°01.2'S, 171°44.4'E, 206–211 m, 4 shells, MNZ M.118312.—Southeast of Great Island, Three Kings Islands, 34°14.1'S, 172°09.0'E, 192–202 m, 7 shells, MNZ M.118311.—Off Northeast Island, Three Kings Islands, 34°08.5'S, 172°11'E, 100 m, 1 shell, MNZ M.34409.—North of Three Kings Islands, 34°01'S, 172°07'E, 700 m, 8 shells, ex MNZ M.34687.—Off Three Kings Islands, 34°10'S, 172°12'E, 250 m, 9 shells, MNZ M.34082.—11 km northwest of Great Island, Three Kings Islands, 34°06.5'S, 172°04.7'E, 310 m, 13 shells, MNZ M.118154.

Distribution: North of New Zealand, around Three Kings Islands; depth range 100–790 m (shells), living specimens not known.



Explanation of Figure 19

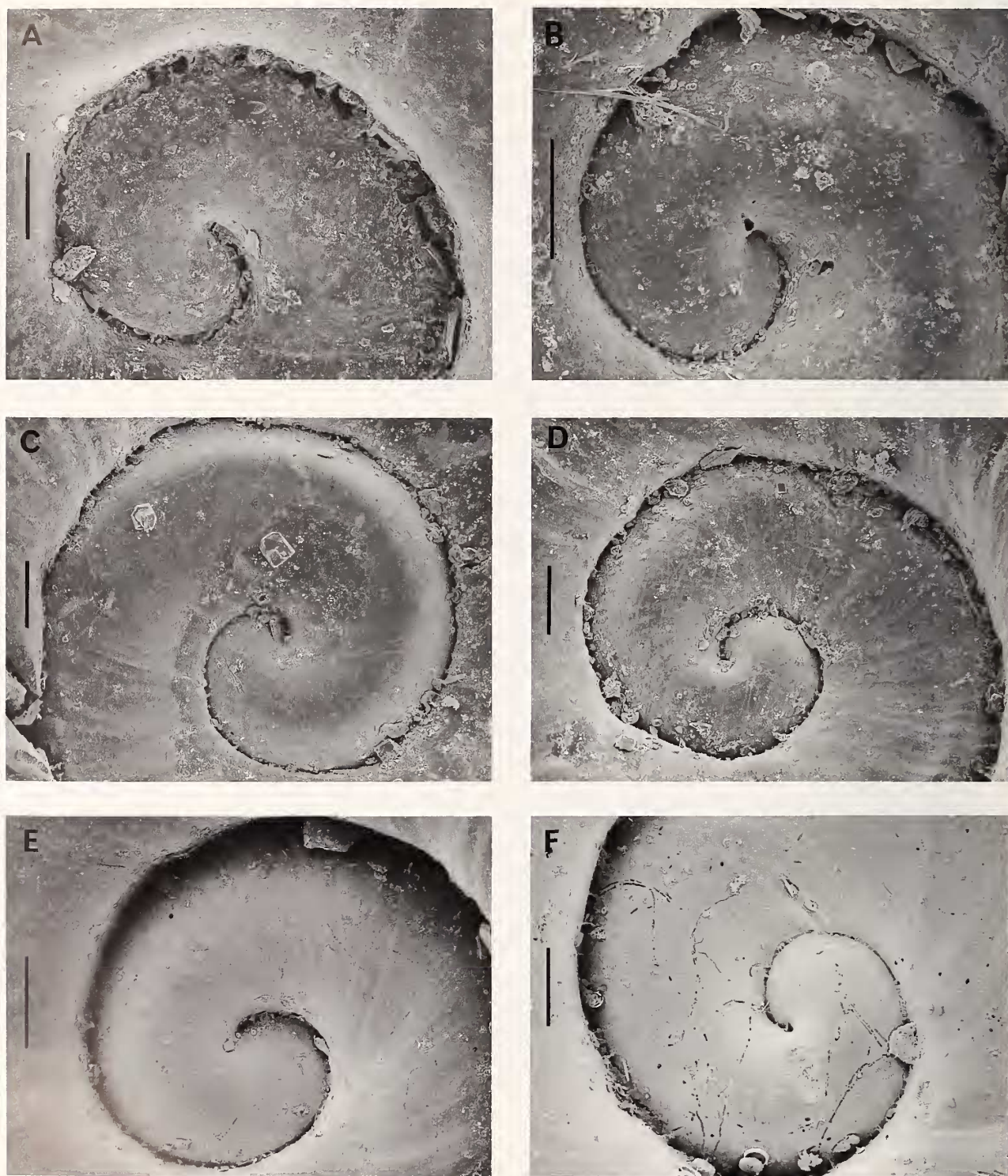
Figures A–C. *Zerotula hedleyi*, MNZ M.33660. Diameters 1.3, 1.6 and 1.3 mm. Figures D–F. *Zerotula coronata* Warén & Hain, sp. nov., paratypes, MNZ M.118852. Diameters, 1.3, 1.3, and 1.4 mm.

Etymology: “*coronatus*” (Latin), with a crown.

Description: Based on shells only.

Shell (Figure 19D, E) very small, vitreous, planispiral, three-keeled, of rapidly increasing diameter. The proto-

conch (Figure 20E) is not clearly set off; its earlier part is smooth, later there are incremental lines, which form a gradual transition to the teleoconch sculpture. The cross section of the whorls is circular internally; their circumference is distinctly pentagonal with three peripheral, strong



Explanation of Figure 20

Zerotula spp., early whorls. Figure A. *Z. nummaria*, MNZ M.59448. Figure B. *Z. bicarinata*, MNZ M.66015. Figures C, D. *Z. triangulata* MNZ M.118148. Figure E. *Z. coronata* Warén & Hain, sp. nov., MNZ M.118852. Figure F. *Z. hedleyi* MNZ M.33660. Scale lines = 50 μ m.

nodulose keels and two sharp corners beside the connection to the preceding whorl. The only additional sculpture consists of irregular growth lines of varying strength.

Dimensions. Diameter of holotype 1.30 mm, maximum diameter 1.40 mm.

Remarks: *Zerotula coronata* is most similar to *Z. hedleyi*, but differs in having distinct tubercles on the keels.

Zerotula stellapolaris Warén & Hain, sp. nov.

(Figures 4B, C, 15C–E, 21A–C, 22C, 23)

Type locality: PS IX/3, sta. 179, 69°58.9'S, 08°00.7'E to 69°59.3'S, 07°59.9'E, 185–161 m, 22 February 1991.

Type material: Holotype and 34 paratypes in SMNH, nos. 4660 and 4661.

Material examined: PS VII/4 sta. 271, 020°W, 399–352 m, 1 specimen.—PS VII/4 sta. 284, 013°W, 402–412 m, 2 specimens.—PS IX/3, sta. 165, 003°W, 191–204 m, 1 shell.—PS IX/3, sta. 173, 007°E, 739–765 m, 5 specimens, 5 shells.—PS IX/3, sta. 174, 010°E, 432–432 m, 3 specimens, 58 shells.—PS IX/3, sta. 180, 006°E, 280–298 m, 24 specimens, 6 shells.—PS IX/3, sta. 206, 010°E, 343–338 m, 1 specimen, 1 shell.—PS IX/3, sta. 207, 005°E, 213–210 m, 2 shells.—PS IX/3, sta. 211, 005°E, 661–742 m, 4 shells.—PS IX/3, sta. 212, 003°E, 568–644 m, 3 specimens, 9 shells (all in SMNH).

Distribution: Only known from the material examined, from the Weddell and Lazarev seas, 21°W eastward to 11°E, depth 190–765 m.

Etymology: “*stella polaris*” (Latin), North Star, German “Polarstern.”

Description: Based on the material above; several decalcified specimens, and sections of two adult female and two adult males.

Shell (Figure 21A–C) small, transparent, planispiral, rather high with angular whorls and conspicuous periostracal keels. The protoconch (Figure 15C–E) is not demarcated from the teleoconch and lacks distinct sculpture. It is distinguishable in very young specimens and consists of about 1 whorl, diameter 0.4 mm. The proto- and teleoconch together form 2.1 whorls of rapidly increasing diameter, sculptured by irregular incremental lines and three strong spiral keels. The two lateral keels are situated close to the periphery at 75% of the radial width of the whorl. The aperture is squarish to rounded with sigmoid peristome. The periostracum is thin, straw-colored, and forms a narrow ridge on the median spiral keel.

Dimensions. Diameter of holotype 1.90 mm (maximum diameter).

External morphology of soft parts: The head-foot and pallial complex comprise almost half a whorl in a contracted specimen, the visceral mass 1.5 whorls. The head-foot is pale beige, the visceral mass more brownish (in

alcohol). Its anterior $\frac{1}{10}$ whorl is paler and contains the kidney and the albumen gland of the oviduct. At the left side, the pericardium (sometimes strongly iridescent; contents of sperm?) with the ventricle and auricle lies directly behind the gill and osphradium. The gonad is not easily distinguished externally, although the specimens are sexually mature. The esophagus and stomach can be seen by transparency, a little more than half a whorl from the operculum, lying obliquely across the left side.

The columellar muscle is inconspicuous and projects slightly at the right and left side of the body, 90–100° from the operculum; dorsally it reaches less than $\frac{1}{2}$ of the height of the whorl and is thus mainly ventral. Its left part is much less conspicuous and narrower.

The pallial cavity is quite deep, and the pallial skirt normally covers the whole head-foot in preserved specimens. The pallial margin is thin and simple, without tentacles and papillae. The osphradium is paralleled by two ridges and runs along the gill from its most posterior part, forward to the anterior $\frac{1}{4}$ of the gill. The gill consists of a series of about 10 small tubercles; the gill width corresponds to $\frac{1}{10}$ of the pallial cavity. The hypobranchial gland is rather inconspicuous. The pallial oviduct is restricted to the posterior right half of the cavity, and its left side contains the rectum, which opens at the same level as the duct.

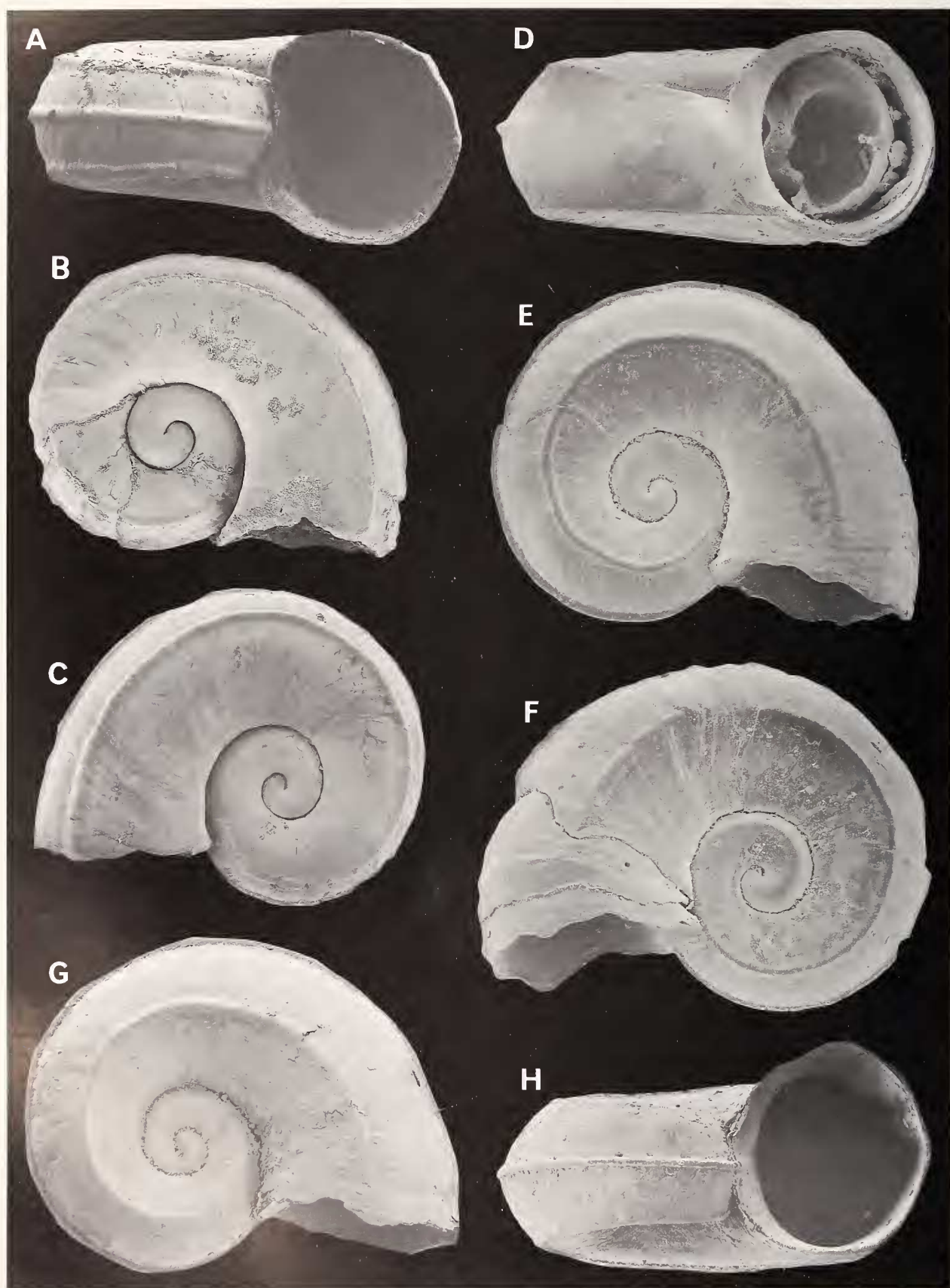
The head is medium-sized, has a pair of slender tentacles, twice as long as the snout. The eyes lack pigment and can be seen as more transparent, round structures in the base of the tentacles. The snout is rather short, slightly tapering, somewhat flattened with a subventral mouth. Males have a simple penis below the right cephalic tentacle.

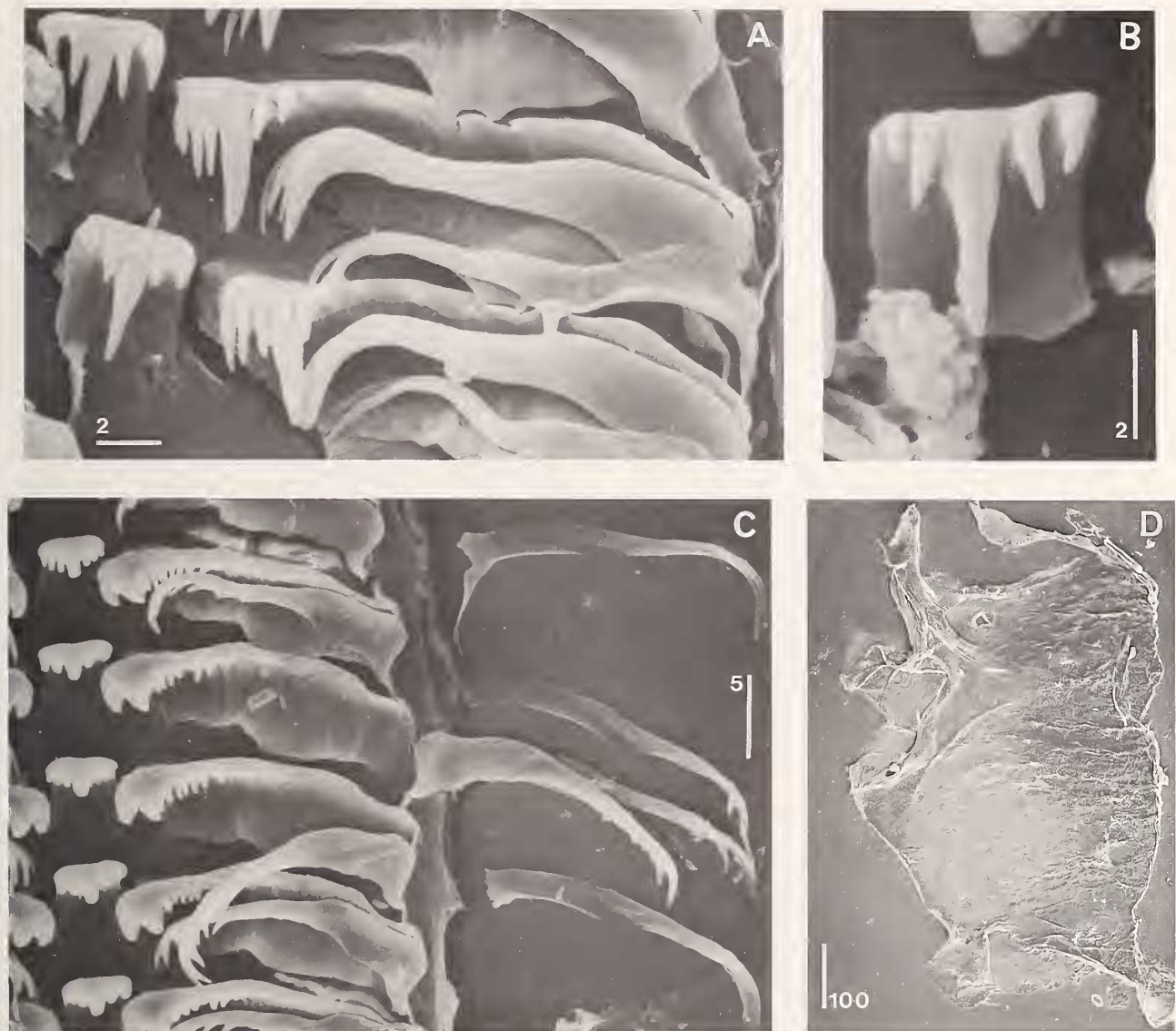
The foot is strongly contracted in all specimens, and the details of its shape could not be discerned. Anteriorly, between the rather poorly demarcated propodium and mesopodium, an anterior pedal gland opens. The sides of the foot are smooth, and there are no epipodial ridges or furrows.

Internal anatomy (Figure 23): The foot (Figure 23B) is almost filled by the large posterior pedal gland and the smaller anterior pedal gland. These bulge a short distance into the cephalopedal haemocoel. The posterior pedal gland stains dark bluish violet, the anterior one, a much lighter grayish violet. The posterior pedal gland has no defined opening. The anterior one has a spacious cavity under the propodium lined with tall epithelium and opens via the slit between the pro- and mesopodium. The muscle layer of the foot is well developed, and the sole is rich in muscle fibers.

The tentacles are solid and muscular, all the way to the base where they have a subcutaneous eye with lens but no pigment layer, in a bulge. The snout is very muscular and can probably be extended considerably when the snail is grazing.

The alimentary system consists of the mouth, a large,





Explanation of Figure 22

Radulae and jaw. Figures A, B. *Z. incognita* Warén & Hain, sp. nov., paratype. Figure C. *Zerotula stellapolaris* Warén & Hain, sp. nov., PS IX/3 sta. 180. Figure D. *Frovina indecora*, PS IX/3 sta. 179, jaw, partly torn. Scale lines in μm .

weakly muscular buccal mass, a very short anterior esophagus, a large esophageal gland, a narrow posterior esophagus, a stomach, intestine, and rectum.

The jaw is thin and membranous.

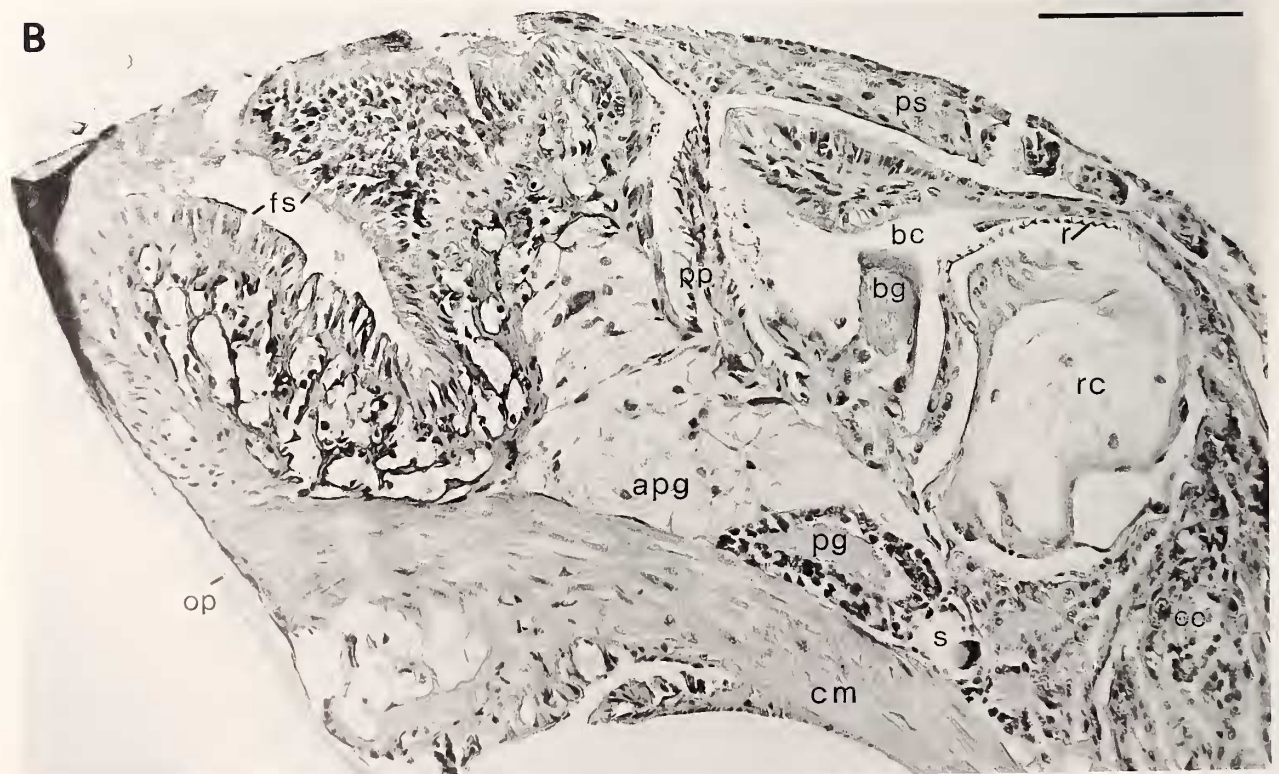
The radular sac is straight, long, and slender, passes backward, through the nerve ring under the esophageal

gland, extending as far back as this. The part of the radula in use is supported by a pair of large cartilages.

Two salivary glands open into the buccal cavity close to its mid-line via short, inconspicuous ducts which do not pass through the nerve ring. The salivary glands are large and situated above the cerebral ganglia. Each consists of

Explanation of Figure 21

Zerotula spp. Figures A-C. *Z. stellapolaris* Warén & Hain, sp. nov., PS VII/4 sta. 284, diameters 1.55, 1.58, and 1.62 mm. Figures D, E. *Z. triangulata* MNZ M.118148, diameters 1.05, 1.18, and 1.19 mm. Figures F-H. *Z. sp.*, Bounty Trough, 45°48.8'S, 174°30.5'E, 1586 m, 26 October 1979, MNZ unregistered, diameter 1.77 mm.



a short, thin duct and a longer, coiled glandular tube. The shallow dorsal food channel is characterized by the rich occurrence of mucus-producing cells. These start in the posterior, dorsal part of the buccal cavity, get displaced toward the left side when passing the nerve ring and end up ventrally in the esophageal gland where they do not reach its posterior end. There seems to be present a pair of esophageal pouches. The interior of the esophageal gland is filled by glandular, transverse septa, which leave only a small ventral lumen for the (now ventral) dorsal food channel. The posterior esophagus exits from the gland as a much narrower, internally strongly ciliated tube of $\frac{1}{5}$ of the diameter of the gland. It continues backward where it ends in a large cavity formed by the openings of the two digestive glands. This cavity opens into the left, ventral, posterior third of the stomach. The stomach measures 0.45 mm long, 0.10 mm high, and 0.15 mm broad. The intestine exits from the anterior part of the stomach, continues obliquely to the right close to the dorsal body wall and behind the kidney. Its diameter is slightly smaller than that of the stomach. Most specimens had remains of forams in the digestive canal.

The nervous system follows the normal pattern, but the dialyneury between the left pleural and the supraesophageal ganglia could not be verified. The distances between the ganglia are very small (contracted specimen), the left pleural and cerebral ganglia partly fused, the right ones abutting. The supra- and subesophageal ganglia are situated less than their diameter from the corresponding pleural ganglion. The length of the connectives to the pedal ganglia corresponds to the diameter of the cerebral ganglia. The supraesophageal ganglion lies free in the left side of the cephalopedal haemocoel behind and beside the left cerebral ganglion; the subesophageal one is well embedded in the body wall slightly farther back. The buccal ganglia are situated dorsally on the buccal mass close to the exit of the esophagus, and connected by a commissure. In front of the pedal ganglia is an accessory pedal ganglion, connected by a short connective, and innervating the anterior pedal gland and propodial area.

Posteriorly and laterally at the base of the penis is a small ganglion, which seems to receive nerves from the right pedal and the subesophageal ganglia (zygoneury).

The visceral ganglia were not identified.

The statocysts (with a single statolith) are situated above and behind the pedal ganglia and slightly displaced to the

right. Their diameter corresponds to the width of the ganglion.

Reproductive system. The sexes are separate, or at least the four specimens sectioned were two males and two females with no trace of intermediate stages. The fixation does not, however, allow any detailed description of the reproductive systems.

Female. The ovary occupies most of the apical 1.5 whorls of the visceral mass. An inconspicuous ovarian duct close to the ventral body wall leads to a large albumen gland, which stains very lightly. It occupies the right third of $\frac{1}{4}$ whorl behind the pallial cavity. In front of this is a capsule gland (staining dark violet), mainly situated in the right wall of the pallial cavity along $\frac{1}{4}$ of a whorl, slightly protruding into and to the right of the anterior part of the albumen gland. The detailed morphology of these could not be worked out due to missing sections. The presence of a gonopericardial duct was confirmed. No receptaculum seminis was found, and no sperm was found in the pericardium of the sectioned females (although one decalcified specimen had a strongly iridescent pericardium as if it were filled by sperm).

Male. The testis lies in the right side of the posterior part of the visceral mass (but does not reach its apex), and is drained by a large, thin-walled duct, which also serves as a vesicula seminalis. About $\frac{1}{4}$ whorl behind the pallial cavity the duct leaves its ventral position and turns into a more laterally and dorsally situated prostate gland. This projects into the right side of the pallial skirt. It seems to be closed and there is no differentiation of cell types in the walls. The prostate is continued by a ciliated duct in the right corner of the cavity. The duct turns to the left, to a long, slender, and tapering penis with a closed sperm duct.

The radula (Figure 22C) is taenioglossate, long, and slender with about 150 transverse rows of teeth and a length corresponding to $\frac{2}{3}$ of the diameter of the shell. The central tooth has a very low and thin, slightly undulating hood. Below this, one major central and three smaller, lateral, rounded cusps form a cutting edge. The "wings" are not drawn out to small denticles at the sides. The front of the tooth is deeply excavated. The lateral tooth usually has about 13 denticles, of which numbers 1 and 3 (counted from the inner edge) are at least three times the size of the others, which form a rather even "comb." The littorinid notch is missing. The first marginal tooth is simple, claw-shaped, with a sturdy shaft and seven apical cusps. The

Explanation of Figure 23

Zerotula stellapolaris Warén & Hain, sp. nov. Figure A. Longitudinal section of right side of head-foot. Figure B. Longitudinal section of central part of head-foot. **ag**—albumen gland; **apg**—anterior pedal gland; **bc**—buccal cavity; **bg**—buccal ganglion; **cc**—cerebral commissure; **cg**—(right) cerebral ganglion; **cm**—columellar muscle; **dg**—digestive gland; **fs**—sole of foot; **oeg**—esophageal gland; **op**—operculum; **ov**—ovary; **pg**—pedal ganglion; **pp**—propodium; **pod**—pallial oviduct; **ps**—pallial skirt; **rc**—radular cartilage; **s**—statocyst; **sn**—snout. Scale lines = 100 μ m.

inner three of these cusps are twice the length of numbers 4–7, which form a series of rapidly diminishing size. The outer marginal tooth is of about the same length, much thinner, with five long apical digits of $\frac{1}{2}$ the length of the tooth. The shaft has an oblique, impressed, shallow furrow starting close to the base and reaching the outer edge of the shaft halfway to the point of the tooth. This probably corresponds to the “joint” in some other zerotulids.

The operculum (Figure 4B, C) has a few whorls, an almost central nucleus, and is transparent, pale brownish yellow, more distinctly so where it is attached to the foot. The surface is distinctly wrinkled by the growth lines.

Remarks: *Zerotula stellapolaris* resembles *Z. triangulata* (Figure 21D, E), from the Three Kings Islands, north of the New Zealand mainland, but that species has the lateral keels situated less close to the periphery, at 50–60% of the radial width of the whorl. That shell also has a more distinctly hyperstrophic coiling than *Z. stellapolaris*.

Zerotula stellapolaris is very similar in shell and radular morphology to a single specimen of a *Zerotula* species (Figure 21F–H) from deep water in the Bounty Trough, east of New Zealand (45°48.8'S, 174°30.5'E, 1586 m, 26 October 1979, MNZ unregistered). That specimen is virtually identical, and we cannot exclude that the peaks of the Macquarie-Balleney Ridge act as stepping stones. We do not, however, have evidence from any other gastropod species that such a connection occurs, but this deep fauna off New Zealand is virtually unknown and there are no hints about such relations among gastropods with more characters in their morphology (B. Marshall, personal communication). Therefore we leave this specimen unidentified so as not to set a precedent in either direction.

Zerotula triangulata Powell, 1937

(Figures 20C, D, 21D, E)

Zerotula triangulata Powell, 1937:209, pl. 54, figs. 15, 16.

Type locality: Off Three Kings Islands, 260 m.

Type material: Holotype in BMNH, not examined.

Material examined: New Zealand, off Three Kings Islands, 34°00'S, 171°55'E, 805 m, 21 shells, MNZ M.118148.—Northwest of Great Island, Three Kings Islands, 34°06.5'S, 172°04.7'E, 310 m, 2 shells, MNZ M.118152.—Southeast of Great Island, Three Kings Islands, 34°14.8'S, 172°13.6'E, 173–178 m, 1 shell, MNZ M.118151.

Distribution: Off northern New Zealand, around Three Kings Islands, depth range 173–805 m (shells only).

Remarks: *Zerotula triangulata* has not been reported since the original description, but the material in MNZ agrees well with Powell's description and figure. As usual in this group, the shell is not very informative. The species is known from empty shells only.

Zerotula nummaria Powell, 1940

(Figures 20A, 24A–E)

Zerotula nummaria Powell, 1940:236, pl. 28, figs. 14, 15.

Type locality: New Zealand, Doubtless Bay, off Awanui, 22 m.

Type material: Holotype in Auckland Museum, not examined.

Material examined: New Zealand, Kapo Wairua, Spirits Bay, shell sand, 6 shells, MNZ M.59448.—Poor Knights Island, northern end of North Island, 32°26.5'S, 178°44'E, 40–45 m, 1 shell, Los Angeles County Museum of Natural History, locality 65–165.—Whangarei, McGregors Bay, 1 shell, MNZ M.20610.—Off Twin Rocks, Bay of Islands, 40–72 m, 1 shell, MNZ M.42208.—Spirits Bay, Kapo Wairua, 2 shells, MNZ M.59448.—Off Three Kings Islands, 34°11'S, 172°10'E, 90 m, 1 shell, MNZ M.33662.—125 m off shore from Motuwheke Island, Bay of Islands, 22–30 m, 1 shell, MNZ M.41898.

Distribution: New Zealand, northeastern North Island (north of 36°S) in 22–90 m (shells only).

Remarks: *Zerotula nummaria* resembles some undescribed species of the genus *Bichoristes* McLean, 1992 (Choristellidae) (McLean, 1992), but is smaller, the shell has a rougher surface, less sharp peripheral keels, and the protoconch is very indistinctly demarcated (sharply demarcated in *Bichoristes*). *Zerotula bicarinata* differs in having an indistinct central keel or at least a keel-like convexity between the two lateral keels.

Zerotula bicarinata (Suter, 1908)

(Figures 20B, 25A–E)

Omalogyra bicarinata Suter, 1908:33, figs. 37, 37a.

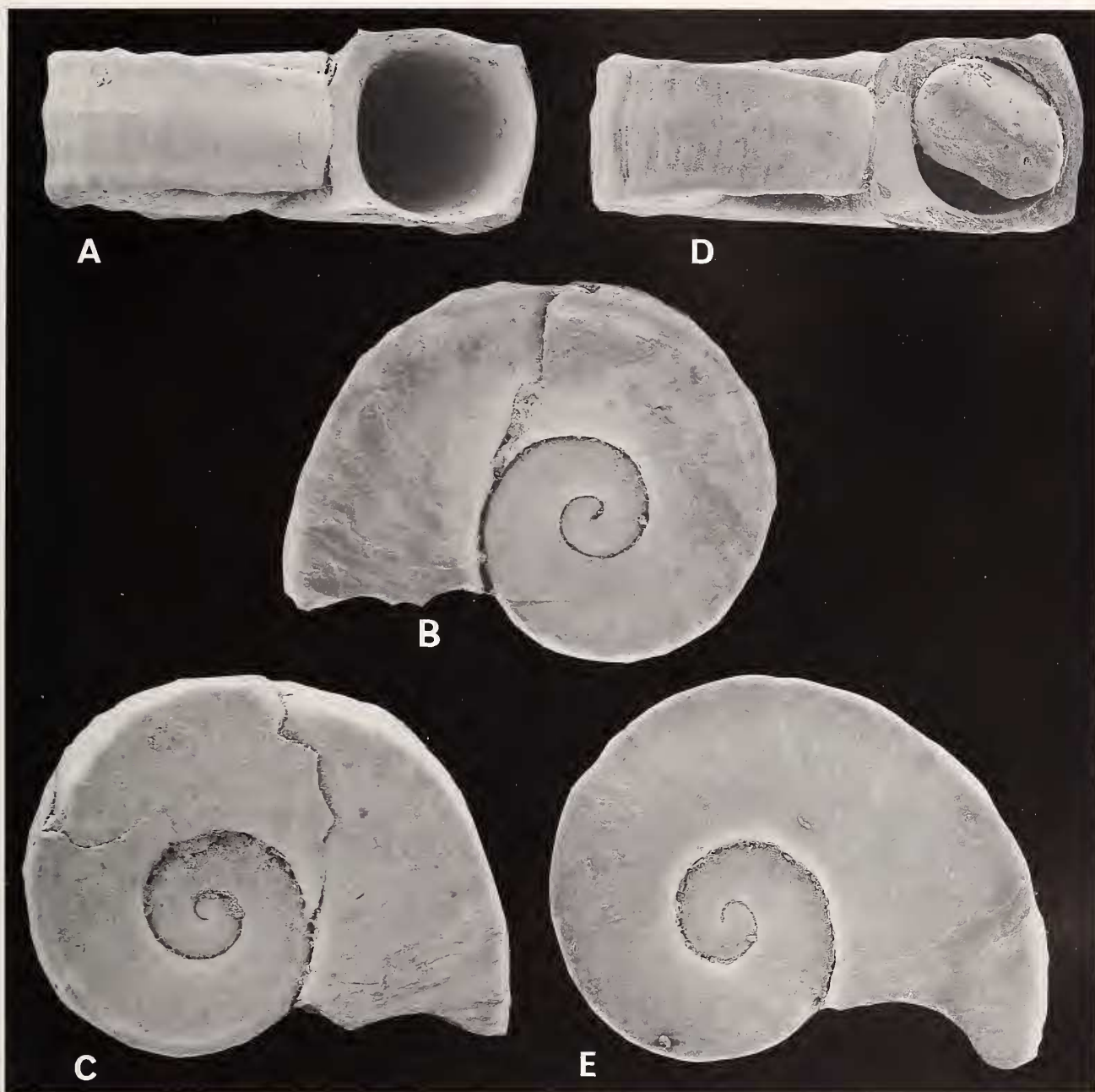
Zerotula bicarinata: Finlay, 1926:379.

Type locality: New Zealand, off Snares Island, 90 m.

Type material: Holotype in coll. Suter, Institute of Geological and Nuclear Sciences, Lower Hutt, not seen.

Material examined: New Zealand, western coast, North Island, off Ahipara, 35°02.6'S, 172°52.6'E, 48 m, 1 shell, MNZ M.118315.

New Zealand eastern coast, East Cape, Ranfurly Bank, 37°33.1'S, 178°49.5'E, 94–89 m, 2 shells, MNZ M.74721.—East Cape, Ranfurly Bank, 37°33.2'S, 178°50.3'E, 76–71 m, 18 shells, MNZ M.72700.—East Cape, Ranfurly Bank, 37°33.4'S, 178°48.3'E, 106–103 m, 2 shells, MNZ M.74804.—Cook Strait, between Pt. Dorset and Pt. Howard, 125 m, 1 shell, MNZ M.44892.—Wellington, Island Bay, 2 shells, MNZ M.18518.—Off East Otago, 45°37.5'S, 171°03'E, 420 m, MNZ M.45582.—East Otago, northeast of Cape Saunders, 45°50'S, 170°56'E,

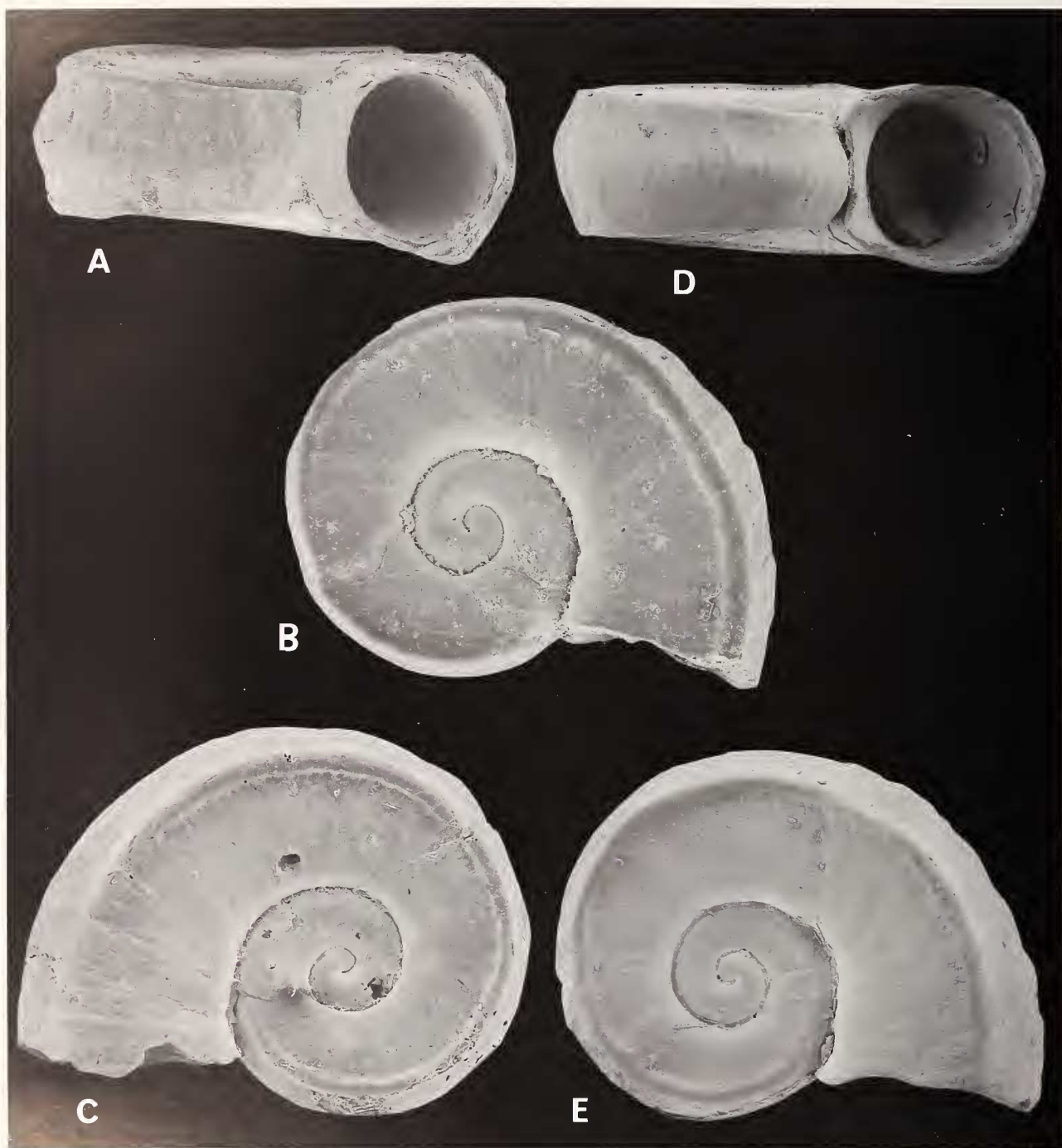


Explanation of Figure 24

Zerotula nummaria. Figures A-C. MNZ M.41848, diameters 1.28, 1.42, and 1.44 mm. Figures D, E. MNZ M.59448, diameters 1.24 and 1.42 mm.

105 m, 2 shells, MNZ M.45334.—Off Otago Heads, 45°50'S, 170°59'E, 220 m, 1 shell, MNZ M.66916.—Dunedin, off Taiere, 46°12'S, 170°41.5'E, 150 m, 6 shells, MNZ M.65876.—Dunedin, off Taiere, 46°09'S, 170°27'E, 60 m, 1 shell, MNZ M.67032.—Dunedin, off Taiere, 46°17'S, 170°32'E, 180 m, 1 shell, MNZ M.66401.—

Dunedin, off Taiere, 46°15'S, 170°29'E, 91 m, 2 shells, MNZ M.66292.—Southeast of Nugget Point, 46°40'S, 170°00'E, 140 m, 6 shells, MNZ M.66015.—Foveaux Strait, 36 m, 1 shell, MNZ M.20606.—Foveaux Strait, 36 m, 1 shell, MNZ M.20603.—Stewart Island, South Cape, Big Ships Passage, 35–65 m, 1 shell, MNZ



Explanation of Figure 25

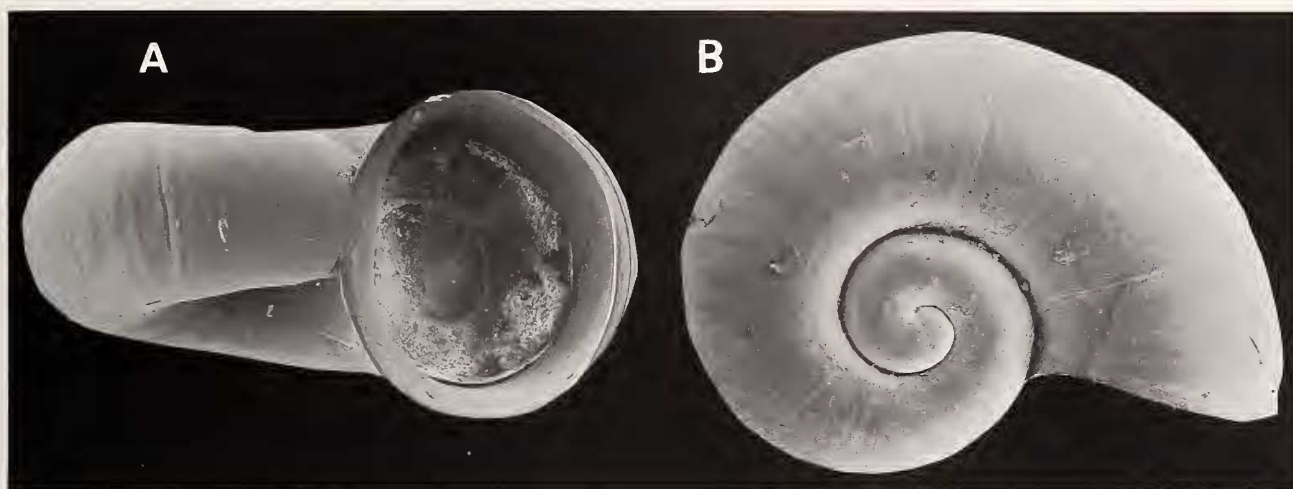
Zerotula bicarinata. Figures A-C. MNZ M.66015, diameters 1.26, 1.12, and 1.41 mm. Figures D, E. MNZ M.20609, diameters 1.6 and 1.5 mm.

M.20684.—Stewart Island, Big S. Cape Island, 90 m, 9 shells, MNZ M.20608.—Stewart Island, off Poutamu Island, 55 m, 3 shells, MNZ M.20609.

Pliocene fossil. Northern bank of Mangahao River, 1 mile south of Mangahao, northern Wairarapa, 31 shells, MNZ M.42687.

Distribution: New Zealand North and South Islands (35–47°S), 35–420 m (shells only).

Remarks: *Omalogyra bicarinata* was included in *Zerotula* by Finlay (1926:379). For differences from *Z. nummaria*, see that species.



Explanation of Figure 26

Figures A, B. *Zerotula incognita* Warén & Hain, sp. nov., holotype, diameter 1.78 mm.

Zerotula incognita Warén & Hain, sp. nov.

(Figures 15F, 22A, B, 26A, B)

Type locality: North Atlantic, off Portugal, ABY-PLAINE CP 13, 40°00.0'N, 15°05.3'W, 5270 m, 8 June 1981, 3 specimens.

Type material: Holotype and one paratype in MNHN.

Distribution: Only known from the type locality, at the Iberia Abyssal Plain, west of Portugal.

Etymology: “*incognitus*” (Latin), unknown, not recognized.

Description: Based on the type series, three dried specimens of which one was sacrificed for preparation of radula and operculum.

Shell (Figure 26A, B) very small, transparent brownish yellow, smooth and planispiral, thin and fragile. The protoconch (Figure 15F) is smooth, not demarcated. The teleoconch consists of about 1.25 whorls and is sculptured by very indistinct, scattered spiral lines and just as weak and irregular growth lines. The peristome is perfectly circular, orthocline, and radial. The whorls are just barely indented by the preceding whorl.

Dimensions. Diameter of holotype 1.78 mm.

Radula (Figure 22A, B). Long and slender. The central tooth (Figure 22A) has two minor cusps on each side of the long and slender main cusp and lacks a hood. The lateral tooth is not clearly visible in our preparation, but as in all *Zerotula* species, there are two main cusps, in this case with two minor ones between them. The inner marginal is long and slender with at least two long apical denticles. The outer marginal tooth is extremely slender, bends at the middle of its length, and has at least two long apical cusps.

Operculum. Circular, thin and colorless, with subcentral nucleus and about three whorls.

Remarks: This species was recognized by the senior author some 13 years ago as being something strange, but since it could not be satisfactorily classified and was believed to be a larva, it was not treated by Bouchet & Warén (1993). It is the only zerotulid we have encountered outside the Antarctic-New Zealand-New Caledonian area.

We can not entirely disregard the possibility that this is a veliger larva, since the shell is characteristically yellowish, thin, and semitransparent. We do not, however, know any gastropod from the North Atlantic with a protoconch that fits this assumption. Moreover, if it is a larva, the presence of a radula indicates that it is ready to metamorphose, and the similarity in radular morphology is close enough to be quite certain it is related to the Zeratulidae.

Species excluded from *Zerotula*

Zerotula crenulata Powell, 1937

Zerotula crenulata Powell, 1937:209, pl. 54, figs. 6, 7.

Type locality: New Zealand, off Three Kings Islands, 260 m.

Type material: Holotype in BMNH (not examined).

Remarks: On the basis of the material examined (MNZ), this seems to be a species of *Adeuomphalus* Seguenza, 1876 (Archaeogastropoda, Family uncertain: Warén 1991:74), or (much less likely) a species of *Zerotula*, similar to *Z. nummaria*.

Zerotula ramosa Powell, 1940

Zerotula ramosa Powell, 1940:237, pl. 29, fig. 3.

Type locality: Off North Cape, New Zealand, 135 m.

Type material: In Auckland Museum, not examined.

Remarks: On the basis of the material examined (MNZ), this is certainly a species of *Palazzia* Warén, 1991 (Archaeogastropoda, systematic position uncertain, Warén 1991:75).

Zerotula ammonitoides Powell, 1940

Zerotula ammonitoides Powell 1940:236, pl. 29, figs. 1, 2.

Type locality: New Zealand, Mangonui, Doubtless Bay, 10–18 m.

Type material: Holotype in the Auckland Museum, not examined.

Remarks: From the material examined (MNZ), this is most likely an omalogyrid, possibly an orbitestellid (Heterobranchia).

Zerotula nautiliformis Powell, 1927

Zerotula nautiliformis Powell, 1927:118, pl. 21, fig. 5.

Type locality: New Zealand, SW of Otago, off Puysegur Point, 310 m.

Type material: Holotype in Canterbury Museum, Christchurch.

Remarks: From material examined, this certainly looks like a species of *Palazzia* Warén, 1991 (Archaeogastropoda, systematic position uncertain, Warén 1991:75).

Dickdellia Warén & Hain, gen. nov.

Type species. *Corneolitorina labioflexa* Dell, 1990.

Etymology: Named after Richard Kenneth Dell (MNZ), who described the only species of the genus.

Diagnosis: Large zerotulids with a poorly calcified, depressed, smooth and rounded shell. Radula long and slender with square, hooded, multicusped central tooth; lateral without “littorinid notch”; outer marginal tooth simplified. Operculum mesospiral without ridge. No metapodial tentacles. Snout small; cephalic tentacles connected by skin fold; mesopodium large and thin, anteriorly drawn out to tentaclelike corners; penis simple, situated well below the right cephalic tentacle; pallial oviduct without bursa and receptaculum.

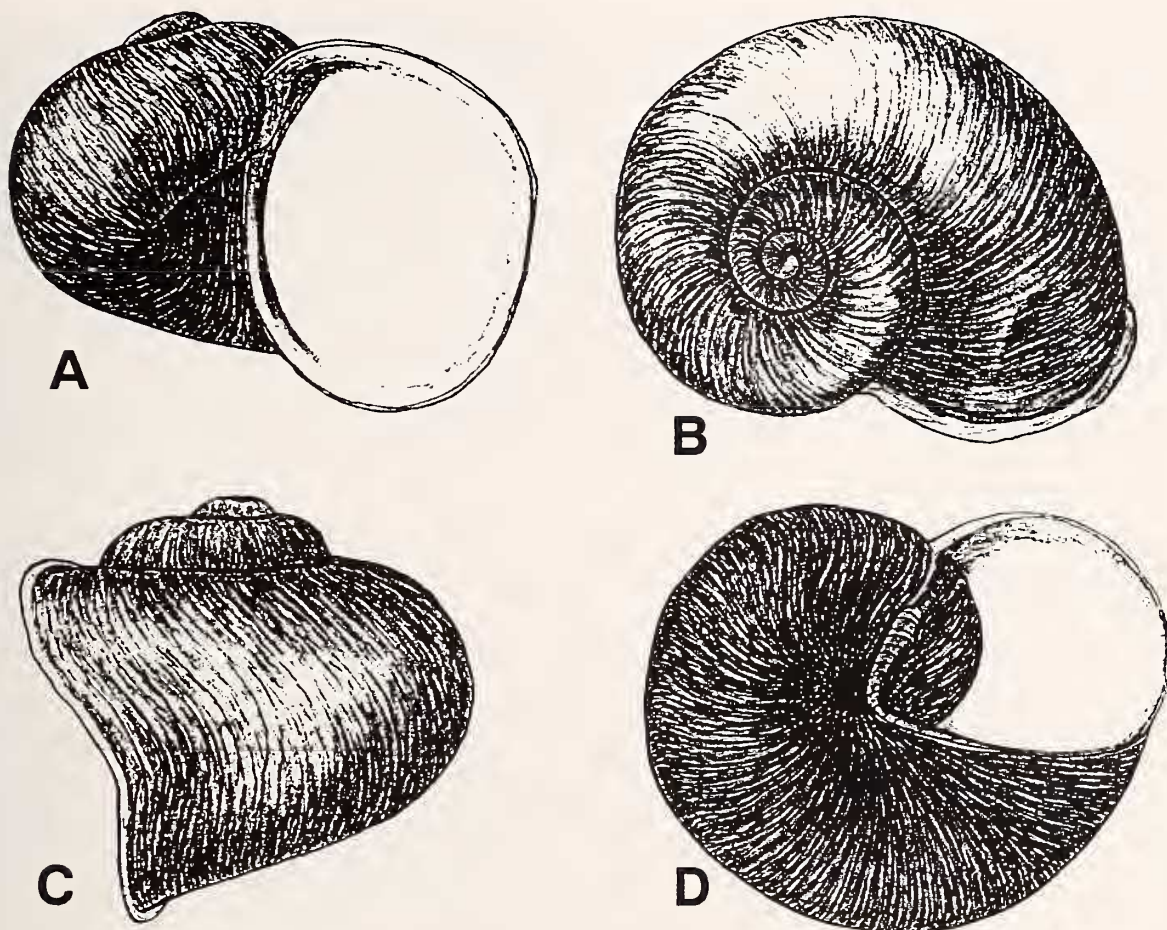
Remarks: *Dickdellia labioflexa* was originally described in *Corneolitorina* Powell, 1951, a generic name considered a synonym of *Laevilitorina* by Reid (1989). The type species of *Corneolitorina* is *Littorina coriacea* Melvill & Standen, 1907, which has a much more normal littorinid-type radula. We agree with Reid (1989) that *L. coriacea* is similar to *Laevilitorina*, and the present resolution of that clade does not necessitate recognition of a genus level name for *L. coriacea*.

We had access to some live-taken specimens, and to give the systematic position a more stable foundation, we examined the anatomy in some detail. This work was dif-

ficult, however, since the specimens had been frozen (because of the temperature during the fieldwork) and were then “fixed” in alcohol. Therefore the whole visceral mass was in a state of disintegration. The results are presented under the species heading.

Systematic position: Several characters of *D. labioflexa* are unusual or strange, to some extent misleading, also in comparison with other zerotulids. Below we list those that have been important for our decisions.

- The shell is very simple and the reduction of the calcareous layer, apomorphic.
- The long and slender radula is consistent with a position among the Littorinoidea.
- A “hooded” radula is unusual. It is known from the Cingulopsidae (see Ponder & Yoo, 1980, fig. 14H) and the Zeratulidae (see above). Its occurrence in *Littoraria* (Littorinidae) was considered apomorphic by Reid (1989: 52).
- The foot has the anterior corners drawn out to tentaclelike protrusions. This is common among archaeogastropods, some higher Neotaenioglossa, and some Neogastropoda, but we know it from the lower neotaenioglossates only in the Litiopidae (Houbrick, 1987; A. Warén, unpublished in *Stiliferina*). In *Stiliferina*, these tentacles do not look like drawn-out corners, but more like set-off tentacles, and may not be homologous.
- The penis, situated well below the cephalic tentacles, indicates a systematic position within or in the vicinity of the Littorinoidea, unless this is a convergence. The innervation could not be examined since we had no male to section.
- The alimentary system with a snout, long taenioglossate radula, a pair of radular cartilages, posterior salivary glands, esophageal gland, agrees with the lower taenioglossates; absence of crystalline style with the Littorinoidea.
- A skin-fold uniting the tentacles is not common among Neotaenioglossa with a snout. It occurs among the Adeorbidae (Rissooidea), Naticidae, and Fossariidae (Cerithioidea). A similar but incomplete fold is present in *Lacuna vineta* (Figure 33A, B) and *L. pallidula*. It is, however, a simple structure and homology is uncertain.
- The nervous system follows the general littorinoid-rissooid pattern, with moderate distances between the ganglia. Presence of two accessory pedal ganglia at each main ganglion resembles Littorinidae, but is also known from the Provannidae (Warén & Ponder, 1991) and Rissoidae (Johansson, 1939) and may be plesiomorphic.
- Absence of receptaculum seminis is rare in the littorinoid-cingulopsoid-rissooid radiation, but known from *Pellilitorina*, *Lacuna*, and *Cremnoconchus* (sperm stored in oviduct, Reid, 1989:36) and most of the zerotulids.
- The general structure of the osphradium is shared with most Littorinoidea-Rissooidea, but the apical flexure is known only from the genus *Lacuna* (Reid, 1989).



Explanation of Figure 27A-D

Dickdellia labioflecta, PS III/3, sta. 345, diameter 7.7 mm.

- The length of the pleural sub- and supraesophageal connective is about eight times the length of the latter ganglia, which is similar to the littorinids (Reid, 1989). This length, however, seems better correlated with the size of the gastropod (both long in *Pomatias elegans* and Littorinidae; short in Zeratulidae (this study) *Skeneopsis*, Risssoidea and Cingulopsidae; one of them long, one short in Aciculidae and Eatoniellidae (Reid, 1989).
- The habitat is considerably deeper than any littorinid (approx. 200–900 m versus 0–50 m), but the presence of eyes indicates that *Dickdellia* does not originate from a group with exclusive deep-water distribution, especially since it has lecithotrophic development.

Of these characters, we pay special attention to the position and shape of the penis, long and slender radula, laterals without littorinid notch, an interspace between the two marginal teeth, and place *Dickdellia* in the Zeratulidae (Littorinoidea).

***Dickdellia labioflecta* (Dell, 1990)**

(Figures 27–29, 30A, B, 31, 32, 34E)

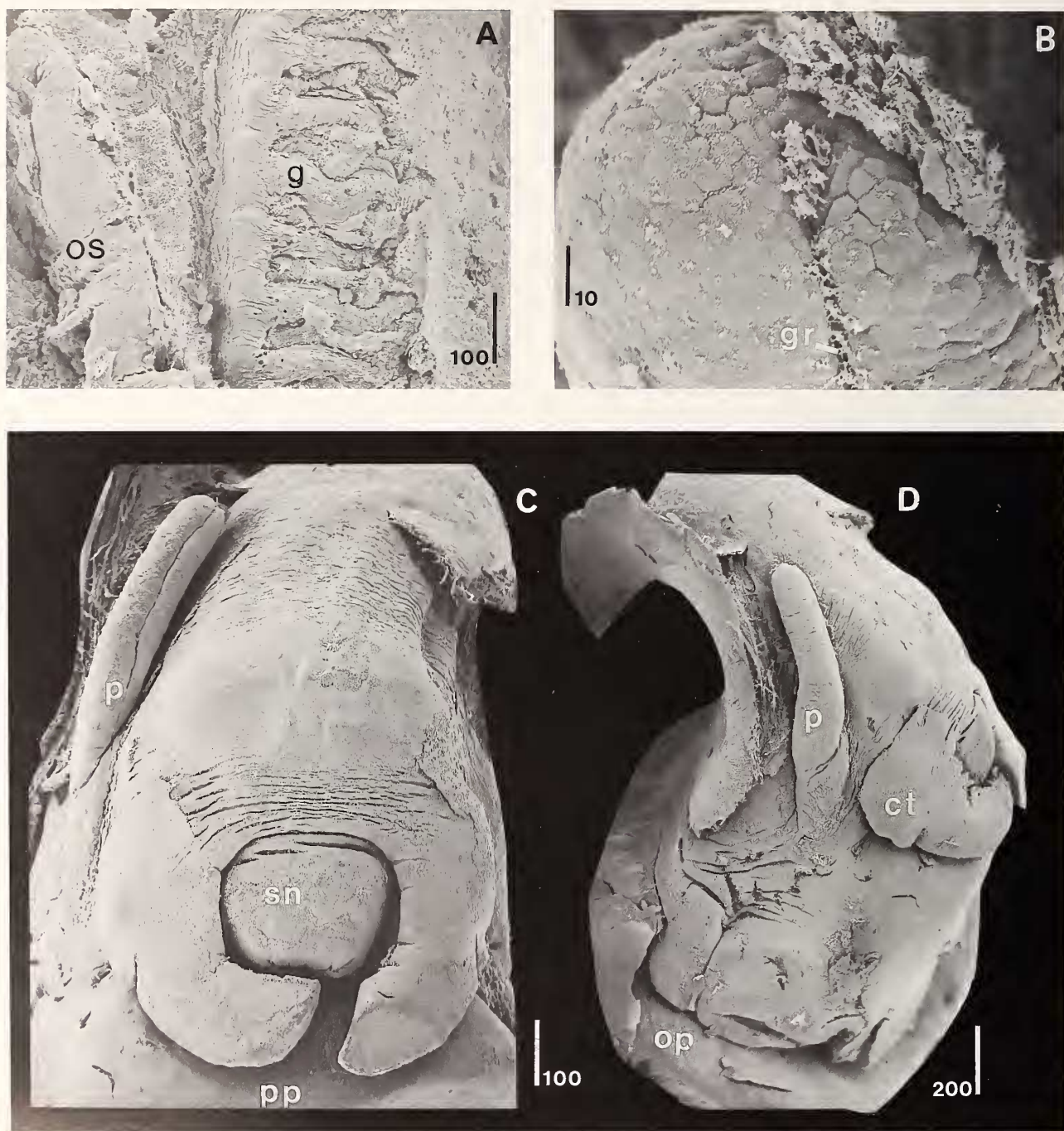
Corneolitorina labioflecta Dell, 1990:110, figs. 187, 188.

Mesogastropoda sp. 2: Hain 1990:54, pl. V, figs 1a–d, pl. 22, fig. 6.

Type locality: Ross Sea, off Elephant Island, *Eltanin* sta. 410, 61°18'S, 56°09'W, 220–240 m.

Type material: Holotype USNM 860099, paratypes USNM 860100 and MNZ MZ.56598, not seen.

Material examined: PS III/3, sta. 345, 021°W, 617 m, 2 specimens.—PS VII/4, sta. 282, 012°W, 609–575 m, 3 specimens.—PS VII/4, sta. 250, 030°W, 799–810 m, 2 specimens.—PS VII/4, sta. 272, 022°W, 409–406 m, 1 specimen. 3.8 mm diameter.—PS VII/4, sta. 293, 012°W, 771–793 m, 1 specimen.—PS VIII/5, sta. 491, 022°W, 390–370 m, 1 specimen. 6.8 mm diameter (all in SMNH).



Explanation of Figure 28

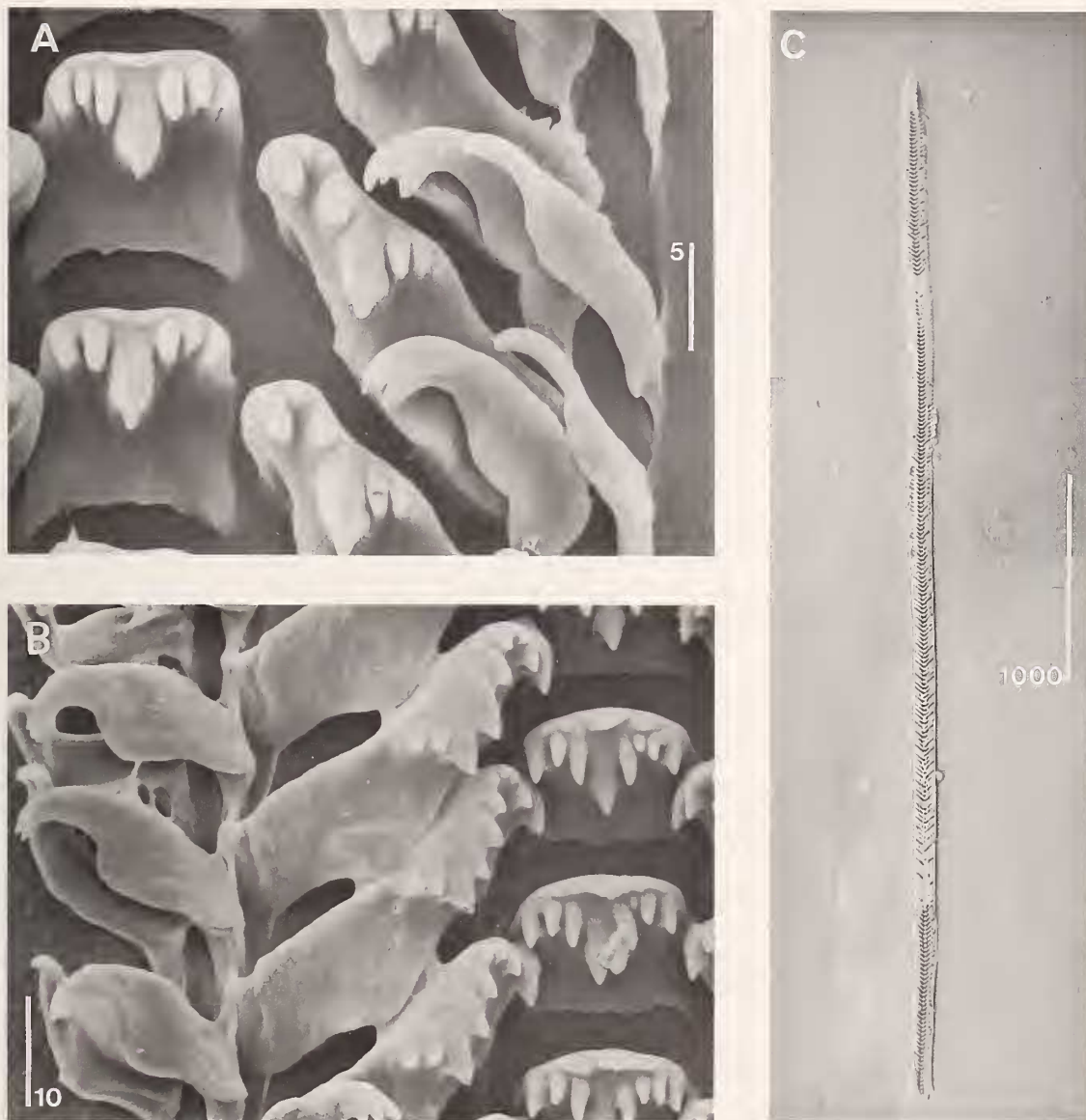
Dicksdellia labioflecta, PS VII/4 sta. 293, critical point dried. Figure A. Part of pallial skirt with gill and ospradium. Figure B. Tip of penis with seemingly open sperm duct. Figure C. Front view of head-foot. Figure D. Right side of head-foot. ct—cephalic tentacle; g—gill leaflet; op—operculum; os—ospradium; p—penis, seminal groove visible in Figure C; pp—propodium; sn—snout. Scale lines in μm .

Distribution: South Shetland Islands, Ross Sea, and the Weddell Sea in 220–891 m.

Redescription: Based on the specimens above of which four females were sectioned, one male critical point dried,

and one female was dissected. The shell (Figure 27), which measures up to 8.3 mm in diameter, was adequately described by Dell (1990), and we give only some supplementary details.

Shell (Figures 27, 34E). The periostracum is thick (0.1



Explanation of Figure 29

Dickdellia labioflecta, PS VII/4 sta. 293, radula. Figure A. From a specimen of 2.5 mm shell diameter. Figures B, C. From a specimen of 6 mm shell height. Scale lines in μm .

mm), brown and tough, slightly brittle. The internal calcareous layer is very thin, less than $5\ \mu\text{m}$ thick at the periphery of the body whorl, thicker toward the columella, and in the two, most apical whorls where it is about as thick as the periostracum.

External morphology of soft parts: The head-foot (Figure 28C, D) and pallial complex (Figure 28A) comprise $\frac{3}{10}$ of a whorl in contracted specimens, the visceral mass about two whorls. The whole animal is creamy white, also the visceral mass (in alcohol and alive). The anterior $\frac{1}{10}$ whorl of the visceral mass is still paler from the superficial part of the kidney. At the left side, the pericardium with

the ventricle and auricle, lies directly behind the gill and osphradium. The gonad is not easily distinguished externally even in sexually mature specimens. The esophagus and stomach could not be discerned externally by transparency.

The pallial cavity is quite shallow, and the pallial skirt normally covers the whole head in preserved specimens. The pallial margin is thin and simple, without tentacles and papillae, except at the right and left $\frac{1}{5}$, where it is thicker and with some structure, but the details could not be worked out. The osphradium (Figure 28A) consists of a ridge containing the osphradial ganglion. It parallels the gill from the most posterior part, forward to the anterior

$\frac{1}{4}$ of the gill, where it abruptly curves 180° to the left and returns $\frac{1}{3}$ of its length. Along each side is a narrow, ciliated ridge. The gill (Figure 28A) consists of a series of about 30 narrow, triangular leaflets twice as high as broad and drawn out to a ventral tip. The width of the gill corresponds to $\frac{1}{6}$ of the pallial cavity. The leaflets in its central part are about twice as wide and high as the anterior ones. The columellar muscle projects at the right side of the body, $60\text{--}80^\circ$ from the operculum. Its left part is much less conspicuous and narrower. The hypobranchial gland is rather inconspicuous and partly covered by the tips of the gill leaflets. The pallial oviduct is restricted to the posterior right half of the cavity and its left side contains the inconspicuous rectum which opens shortly behind the oviduct.

The head is medium-sized and has a pair of short (contracted; slender and tapering when crawling), conical, flattened tentacles with large black eyes in basal-lateral bulges. The inner sides of the tentacles meet over the small snout by a simple fold of the outer part of the body wall. The male has a simple, finger-shaped penis situated well below the right cephalic tentacle, and with a dorsal furrow (Figure 28B, D). Whether this furrow forms an open or closed sperm duct could not be seen.

The foot is flat, large, and broad. The corners are drawn out to small tentaclelike extensions. Posteriorly, it is bluntly rounded. There is no distinct opening for the posterior pedal gland; anteriorly, between the distinctly set-off propodium and the mesopodium opens an anterior pedal gland. The sides of the foot are smooth and there are no epipodial ridges or furrows.

Internal anatomy (Figures 31, 32): The foot is almost filled by the large posterior pedal gland mixed with a dense three-dimensional network of muscle fibers. The slightly smaller anterior pedal gland bulges into the cephalopedal haemocoel, shortly behind the nerve ring and into the snout. The posterior pedal gland stains bluish violet, the anterior one a much lighter grayish violet, with conspicuous nuclei. The posterior pedal gland does not have a defined opening. The anterior one has a flat cavity under the propodium, lined with tall epithelium and opens via a broad and flat duct, which penetrates most of the gland.

The anterior part of the tentacles is solid and muscular, but behind the eye there are large lacunae. The large subcutaneous eyes (with lens and pigment layer) are situated in a large bulge in the latero-basal part. The snout is very muscular and can probably be extended considerably when the snail is grazing.

The alimentary system consists of the mouth, a large, thin-walled buccal mass, a very short anterior esophagus, a large esophageal gland, a narrow posterior esophagus, stomach, intestine, and rectum.

There are no jaws. Not even a noticeable cuticular lining was found in or behind the mouth.

The radular sac is straight, rather long, curves to the right after the exit from the buccal mass and ends between

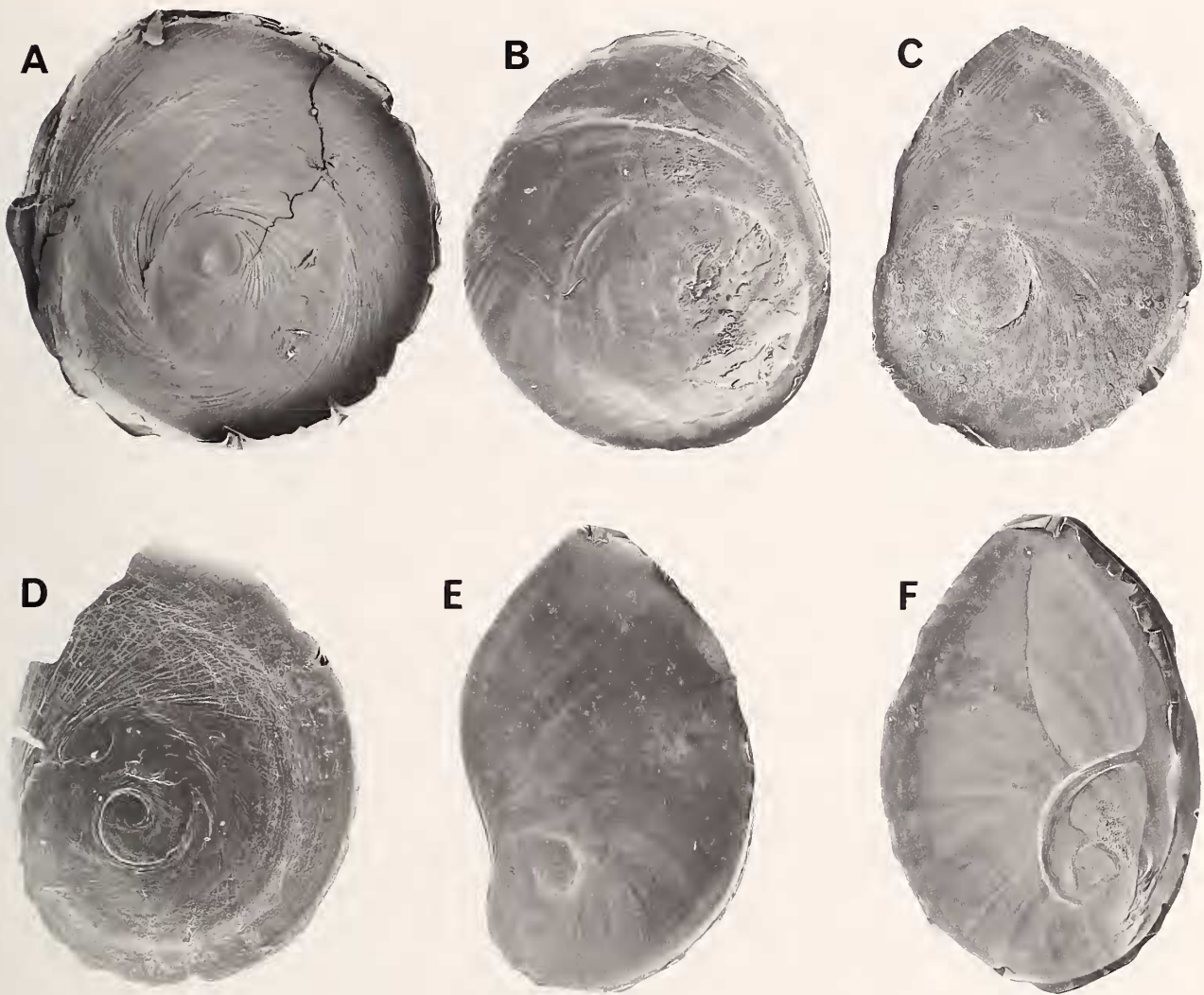
the roof of the cephalopedal haemocoel and the buccal mass. The part of the radula in use is supported by a pair of large, anteriorly diverging cartilages.

Two salivary glands open into the buccal cavity, close to its mid-line, via short, inconspicuous ducts which do not pass through the nerve ring. The salivary glands are large and situated before and above the cerebral ganglia. Each consists of a short, thin duct and a voluminous gland of several lobes (staining violet with EHE). The dorsal food channel is characterized by the occurrence of numerous mucus-producing cells. These cells commence in the postero-dorsal part of the buccal cavity, are displaced toward the left when passing the nerve ring, and end up ventrally in the esophageal gland, where they continue until the start of the posterior esophagus. No trace of esophageal pouches was found. The esophageal gland is quite voluminous and full of transverse septa which leave only a small space for the longitudinal food channel. At the end of the cephalopedal haemocoel, the posterior esophagus exits from the gland, passes the transverse septum and enters the visceral mass. It continues backward, ventrally and close to the body wall at the left side of the body. Finally, it enters the stomach, 0.3 mm from its most posterior part. The diameter of the stomach is about 0.20 mm. The stomach continues forward 0.35 mm, turns abruptly dorsally, a loop 0.5 mm long; then another abrupt turn to the left, for a distance of 0.5 mm, after which it starts paralleling the oviduct in a rectal sinus, which thus by definition must be a rectum. It was not possible to see any distinct transition from a stomach to an intestine between the esophagus and rectum. The rectum is unusually small (Figure 31B, re).

The nervous system follows the normal pattern of littorinids, with dialyneury between the left pleural and the supraesophageal ganglia. The distances between the ganglia are fairly short (contracted specimen), the pleural and corresponding cerebral ganglia abutting. The supra- and subesophageal ganglia are situated about eight times their diameter from the corresponding pleural ganglion. The length of the connectives to the pedal ganglia are twice the diameter of these ganglia. The supraesophageal ganglion lies free at the left wall of the cephalopedal haemocoel, at half its height; the subesophageal one in a pit in the body wall. The buccal ganglia are situated dorsally on the buccal mass, close to the exit of the esophagus, and connected by a commissure. Ventrally and anteriorly to the pedal ganglia is an anterior accessory pedal ganglion, connected by a connective of about its own length and innervating the anterior pedal gland and propodial area. Posteriorly and ventrally there is a posterior accessory pedal ganglion, connected by a connective of half its own length and innervating the meso- and metapodium.

The visceral ganglia were not identified.

The statocysts are situated above and behind the pedal ganglia and slightly displaced laterally. Their diameter corresponds to half the length of the ganglion. They have a single statolith.



Explanation of Figure 30

Opercula. Figures A, B. *Dickdellia labioflecta*, PS VII/4 sta. 293, diameters 3.6 and 3.1 mm. Figure C. *Laevilitorina notorcadensis*, paratype, diameter 2.0 mm. Figure D. *Laevilitorina antarctica*, South Georgia, Cumberland Bay, 1–2 m, on algae, SMNH 2794, diameter 3.9 mm. Figures E, F. *Lacuna vineta*, Swedish west coast, diameter 4.2 and 5.2 mm.

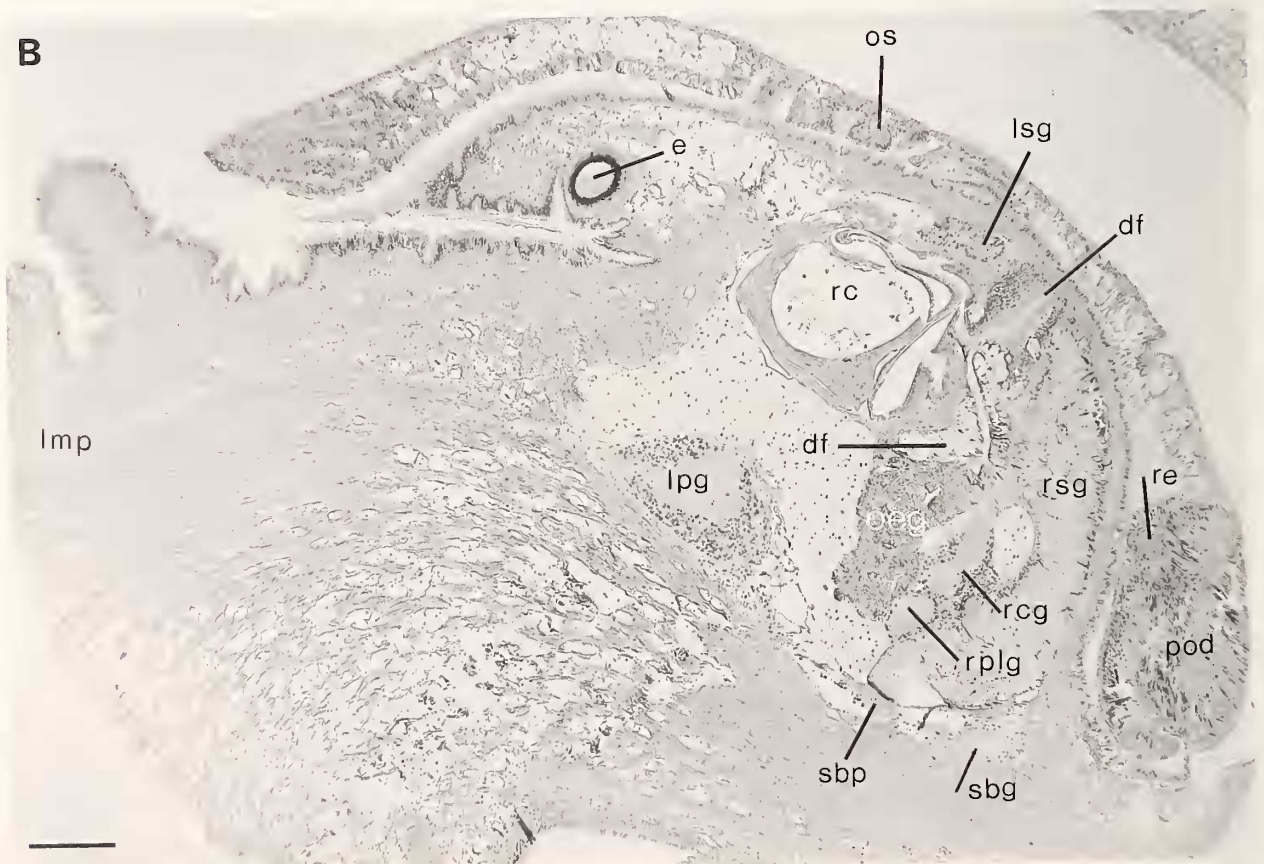
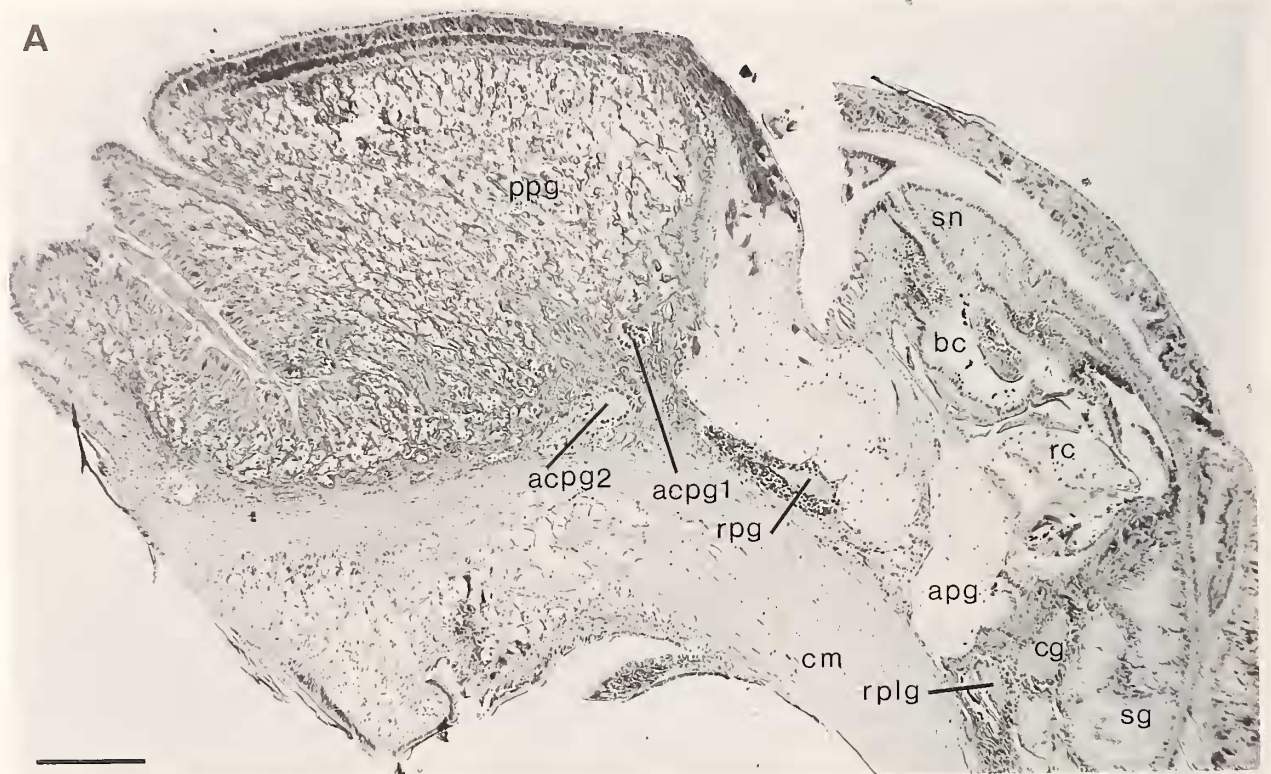
Circulatory system. The pericardium and kidney are unexpectedly small.

Reproductive system. The sexes are separate. One of the sectioned specimens, 3.8 mm in shell diameter, turned out to be a female without pallial oviduct, but with an early ovary and no trace of male systems, while the male used for critical point drying had a shell diameter of 3.0 mm.

The fixation does not, however, allow any detailed description of the female system, and no male was sectioned. The ovary lies along the right side of the visceral mass. A short ovarian duct leads to a large, strongly folded albumen gland, which stains very lightly. Along the anterior right side of this and continuing anteriorly is a capsule gland

(Figure 32B; staining dark violet with EHE), but the detailed morphology of these could not be worked out due to missing and ruptured sections. They are, however, closed except for a short opening close to the anterior end of the capsule gland. No trace of a bursa copulatrix or a receptaculum seminis was found. A well-developed gonopericardial duct is present, opening into the albumen gland close to the ovarian duct. None of the two females that were sectioned had sperm in the pericardium, or a receptaculum seminis, but sperm was abundant in the posterior folds of the albumen gland. External features of the male were described above.

The radula (Figure 29) is long and slender, almost 50



times as long as broad, with about 200 transverse rows (Figure 29C). The central tooth is rather low, distinctly hooded, and has a large, conical main cusp and three similar cusps of half the size on each side, situated above the main cusp. The lateral tooth is long, rather slender, and oblique and lacks a "littorinid notch." The central half is strongly denticulated with about 12 strong subequal cusps. The first marginal tooth is attached slightly in front of the lateral and is quite sturdy with its proximal part twice as broad as its distal third. It has three small apical denticles. The second marginal tooth is slightly smaller than the first marginal, and separated from it by a zone of smooth radular membrane, of a width corresponding to $\frac{1}{20}$ of that of the radula. Its apical third is proportionally narrower than in the first lateral and the apical denticles are smaller. Young specimens have less sturdy and proportionally taller teeth with fewer denticles.

The operculum (Figure 30A, B) is rather sturdy and distinctly wrinkled by incremental lines. It consists of about three whorls with a subcentral nucleus, but lacks a ridge.

Remarks: The smooth, poorly calcified shell with a shallow labial sinus makes this species easily recognizable among Antarctic gastropods.

The remarkably small and slender esophagus, stomach, and intestine, containing very little remains of food, suggest an unusual type of food, not detritivory or forams. This is also suggested by a strange appearance of the digestive gland which has much smaller tubules than usual.

Family LITTORINIDAE

Subfamily LAEVILITORININAE

Reid (1989) gave an exhaustive survey of the classification of the Littorinidae and analyzed the relations within the family. We have extensively used this gold mine of information, and supplemented it with our own observations in some cases.

Laevilitorina Pfeffer, 1886

Laevilitorina Pfeffer, in von Martens & Pfeffer, 1886, type species, *Littorina caliginosa* Gould, 1849, by subsequent designation (Suter, 1913).

(*Pellilacunella*) Powell, 1951

Pellilacunella Powell, 1951, type species *Pellilitorina bennetti* Preston, 1916, by original designation.

Remarks: Reid (1989) recognized a new subfamily for *Laevilitorina* with several subgenera. Among these are *Pellilacunella*, characterized by four opercular tentacles on each side, a simple penis with short filament, numerous small cusps on the rachidian tooth, and a single small cusp on the outer marginal tooth. The shell is simple, smooth, and rounded; the operculum belongs to Reid's (1989) paucispiral type with no internal ridge.

Reid (1989) presented information on most type species of the littorinid generic names. We here add a few details on little known generic names we encountered, to complete Reid's treatment.

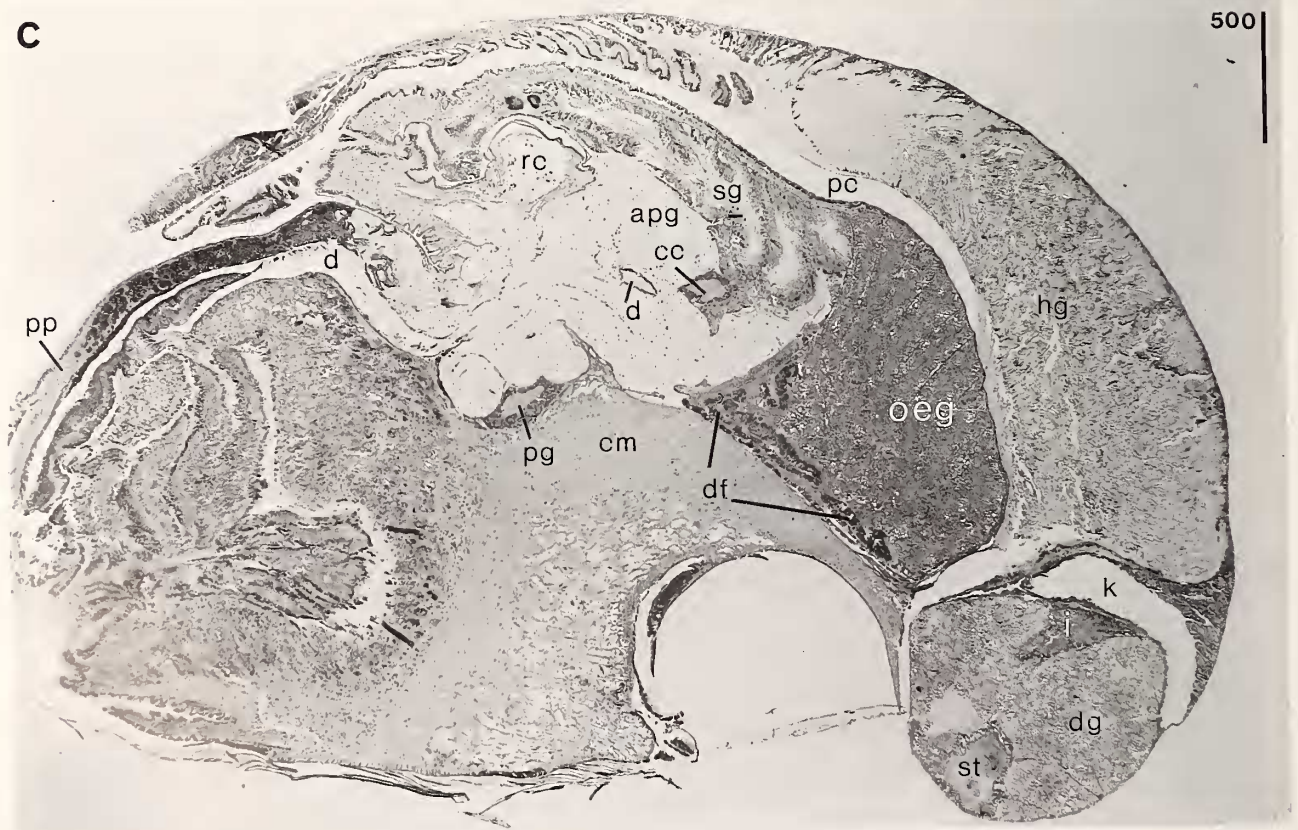
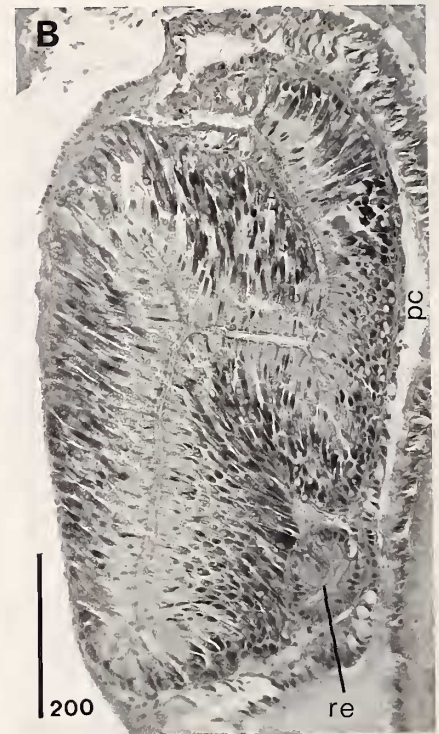
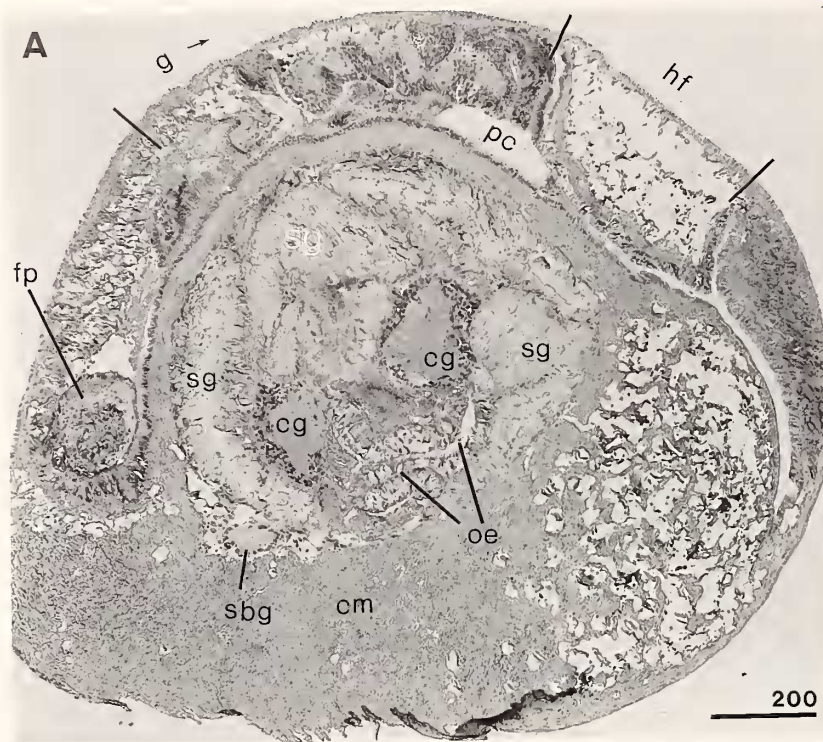
Lacunella reflexa Dall, 1884, and its "variety" *minor* Dall, 1919, were both described from shallow water in Alaska. The former species is the type species of *Haloconcha* Dall, 1886, usually regarded as a genus, but with some hesitation synonymized with *Lacuna* (at subgenus level) by Reid (1989). Our information comes from reconstituted type specimens in USNM. Shell, Figure 34A, B; radula, Figure 35A. The soft parts were not in good condition, but the pair of opercular tentacles are replaced by a thin, wide membrane. The operculum has an unusually low and indistinct opercular ridge, like other Lacuninae. Also, this generic name can thus safely be placed in the Lacuninae, although more information is needed to evaluate its detailed placement there.

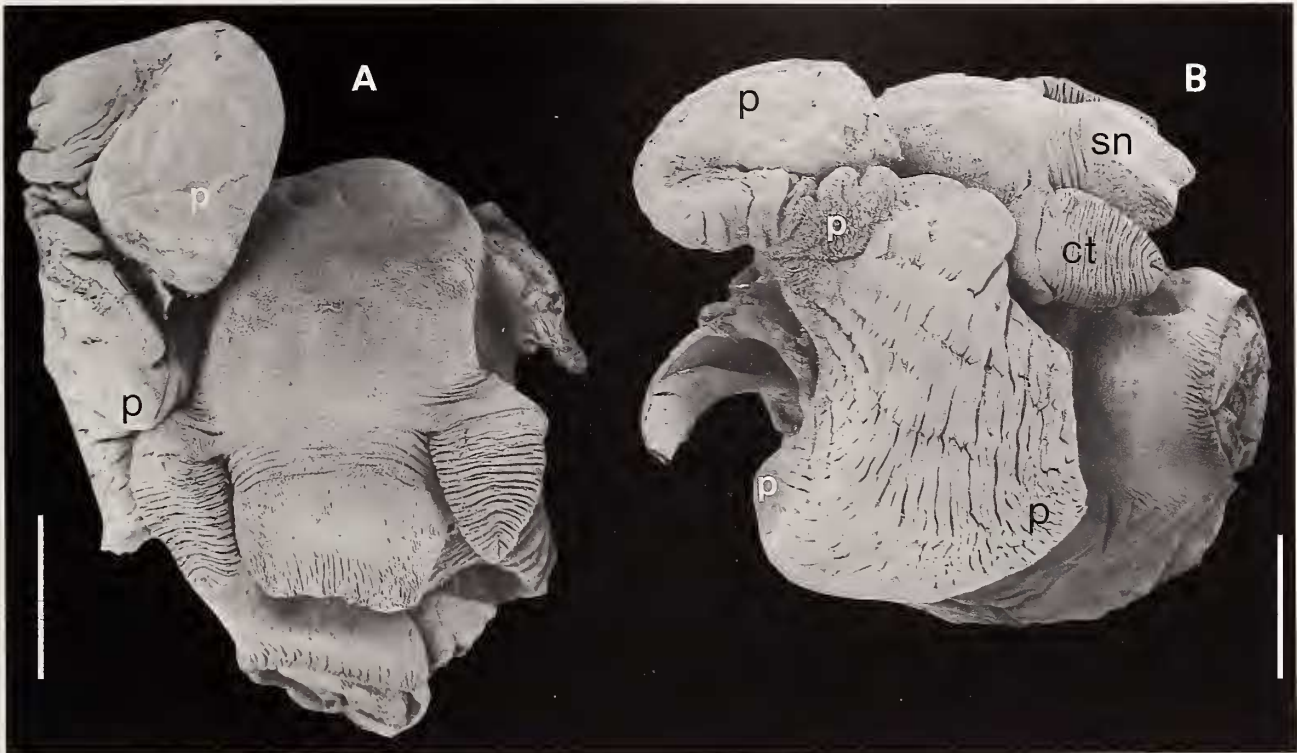
We also examined type material of *Aquilonaria turneri* Dall, 1886, from Alaska, type species of *Aquilonaria* Dall, 1886. Two pairs of opercular tentacles, a ridge on the operculum, well-developed periostracum, and an indistinctly hooded rachidian tooth confirm a position in the Lacuninae and relations to *Lacuna* (*Lacuna*) *crassior* (Montagu, 1803).

Both *Lacuna pallidula* (Da Costa, 1778) and *L. (Epheria) vineta* (Montagu, 1803) (both north European) have a distinct skin fold across the basal part of the cephalic tentacles, continuing a short distance toward the center of the snout. Possibly this is an artifact, but it is persistently there and probably has some internal cause in the arrangement of the muscles.

Explanation of Figure 31

Dickdellia labioflecta. Figure A. Longitudinal section of head-foot to the right of mid-line. Figure B. Oblique cross sections of head-foot, through left eye, further posterior through right side. **acpg1**—propodial accessory pedal ganglion; **acpg2**—mesopodial accessory pedal ganglion; **apg**—anterior pedal gland; **bc**—buccal cavity; **df**—dorsal food channel; **e**—eye; **lmp**—left part of mesopodium; **lpg**—left pedal ganglion; **lsg**—left salivary gland; **oeg**—esophageal gland; **os**—osphradium; **pod**—pallial oviduct; **ppg**—posterior pedal gland; **rc**—radular cartilage; **rcg**—right cerebral ganglion; **re**—rectum; **rpg**—right pedal ganglion; **rrplg**—right pleural ganglion; **rsg**—right salivary gland; **sbg**—subesophageal ganglion; **sbp**—subesophageal pleural connective; **sg**—salivary gland; **sn**—snout. Scale lines = 200 μ m.





Explanation of Figure 33

Lacuna vincta, Koster Area, Swedish west coast. Figure A. Dorsal view of head-foot. Figure B. Right side of head-foot. ct—cephalic tentacle; p—penis; sn—snout. Scale lines = 1 mm.

The penis of *Lacuna vincta* is very large, and we give an SEM photo of a head-foot showing this and the morphology of the cephalic tentacles (Figure 33).

Systematic position of *Lacuna wandelensis*: The combination of undivided foot, presence of metapodial (opercular) tentacles on each side, and a thin, fragile shell are characters of Laevilitorininae with its single genus *Laevilitorina* Pfeffer, 1886; the Lacuninae; and *Lacuna wandelensis*.

For the choice between these two subfamilies, we pay attention to the absence of a spiral ridge on the operculum, presence of four pairs of opercular tentacles, strong resemblance in radular characters and classify *Lacuna wandelensis* in Laevilitorininae, genus *Laevilitorina*, subgenus *Pellilacunella*.

Further details which may or may not mean something are:

(1) We have noticed an apical, fine striation in *L. wandelensis* (Figure 34D), identical to that in *Laevilitorina* (*Macquariella*) *antarctica* (von Martens, 1886) (Figure 34C, H) also in size. We have scanned several true lacunines, which all have smooth apical whorls.

(2) A "hooded" radula occurs also in the Lacuninae, e.g., *Haloconcha* (Figure 35A) and *Lacuna* (*Lacuna*) *crassior* (Montagu, 1803), while the closely related *Lacuna* (*Epheria*) *vincta* Montagu, lacks a "hood" (Figure 35B). The "hood" seems therefore more widely distributed among the littorinids than previously assumed.

←

Explanation of Figure 32

Dickdellia labioflecta. Figure A. Oblique cross section of body at the level of the cerebral ganglia. Figure B. Cross section of pallial oviduct. Figure C. Longitudinal section through head-foot. apg—anterior pedal gland; cc—cerebral commissure; cg—cerebral ganglion; d—duct from anterior pedal gland; dg—digestive gland; fp—fecal pellet; g—part of pallial skirt with gill; hf—pallial skirt fused to head-foot; hg—hypobranchial gland; i—intestine; k—kidney; oe—esophagus; oeg—esophageal gland; pc—pallial cavity; pp—propodium; rc—radular cartilage; sbg—sub-esophageal ganglion; sg—salivary gland; st—stomach. Scale lines in μm .

(3) The radula of *Laevitorina* (*Pellilacunella*) *wandelensis* is more similar to that of the type species of *Pellilacunella* than what is evident from a comparison with Reid's stylized fig. 13a. We have compared with unpublished SEM photos of the radula of *L. (P.) bennetti*, kindly supplied by Reid. The two species share the unique, erect appearance of the rachidian, the lateral, and first marginal teeth. This is also the case in *Laevitorina* (*Macquariella*) *antarctica* (Figure 35D), though to a lesser extent.

Laevitorina (*Pellilacunella*) *wandelensis*
(Lamy, 1905)

(Figures 10D–F, 30C, 34D, 35C, E, F)

Lacuna wandelensis Lamy, 1905:478, fig. 2.

Lacuna wandelensis: Lamy 1906:5, pl. 1, figs. 5–7.

Lacuna notorcadensis Melvill & Standen, 1907:131, fig. 2.

Lacuna wandelensis: Melvill & Standen 1912:349.

Antitrichotropis wandelensis: Powell 1951:124.

Type localities: *L. wandelensis*, Antarctic, Palmer Archipelago, Wandel Island, Port Charcot, 40 m; *L. notorcadensis*, South Orkneys, Scotia Bay, 15–18 m.

Type materials: *L. wandelensis*, Holotype in MNHN, examined; *L. notorcadensis*, Holotype (Figure 10D) RSM 1921.143.623, syntypes (Figure 10E, F), NMWZ 1955.158.157 (see Trew, 1987).

Material examined: Type material of *L. wandelensis* and *L. notorcadensis* and: POLISH ANTARCTIC EXPEDITION 1980, stas. N70 and N119, South Shetland Islands, King George Island, Admiralty Bay, 30–38 m, 2 specimens (from P. Arnaud).

Distribution: South Shetland, Antarctic Peninsula, and South Orkneys, about 10–40 m depth, “on *Macrocytis* and other large fuci” (Melvill & Standen, 1912).

Redescription: We only describe the external morphology of the soft parts, the radula, and the operculum. Shell, Figure 10D–F; protoconch, Figure 34D.

Soft parts. The whole head-foot is blackish green in a dried specimen, especially the snout and tentacles. The head has a large snout, about as long as broad, slightly conical, and with terminal mouth. The cephalic tentacles

are about twice as long as the snout and are distinctly flattened. The eyes are situated close to the base of the tentacles in a low bulge on their outer sides. The penis is short, rounded, fingerlike, situated somewhat below the right cephalic tentacle. The foot has four flattened metapodial tentacles connected by a membrane on each side. The gill has about 20 leaflets in the roof of the unexpectedly deep pallial cavity. The osphradium consists of a low ridge running along and to the left of gill, but this may be composed of more than one ridge, now fused because of the drying. There are no pallial tentacles. The left corner of the pallial edge has two low, indistinct siphonal ridges.

The radula (Figure 35C, E, F) is colorless, about as long as the diameter of shell. The outer marginal tooth is small and narrow, with three to five apical denticles. The inner marginal, lateral, and central teeth are similar to each other, with the cutting edge forming a right angle to the narrower basal plate. At each side and below the broad, straight, weakly serrated cutting edge there is a small denticle. The inner marginal tooth is much larger than the outer one. The lateral tooth has a poorly developed outer lateral process. The central tooth has a hood (partly obscured by the fact that the whole tooth is strongly recurved), a finely serrate cutting edge, a large lateral cusp at each side, and a latero-basal point.

The operculum (Figure 30C) is paucispiral, thin, corneous, without internal ridge.

Remarks: The holotype of *L. wandelensis* is immature, about 2.4 mm high, the type specimens of *L. notorcadensis* are somewhat larger, just below 3 mm.

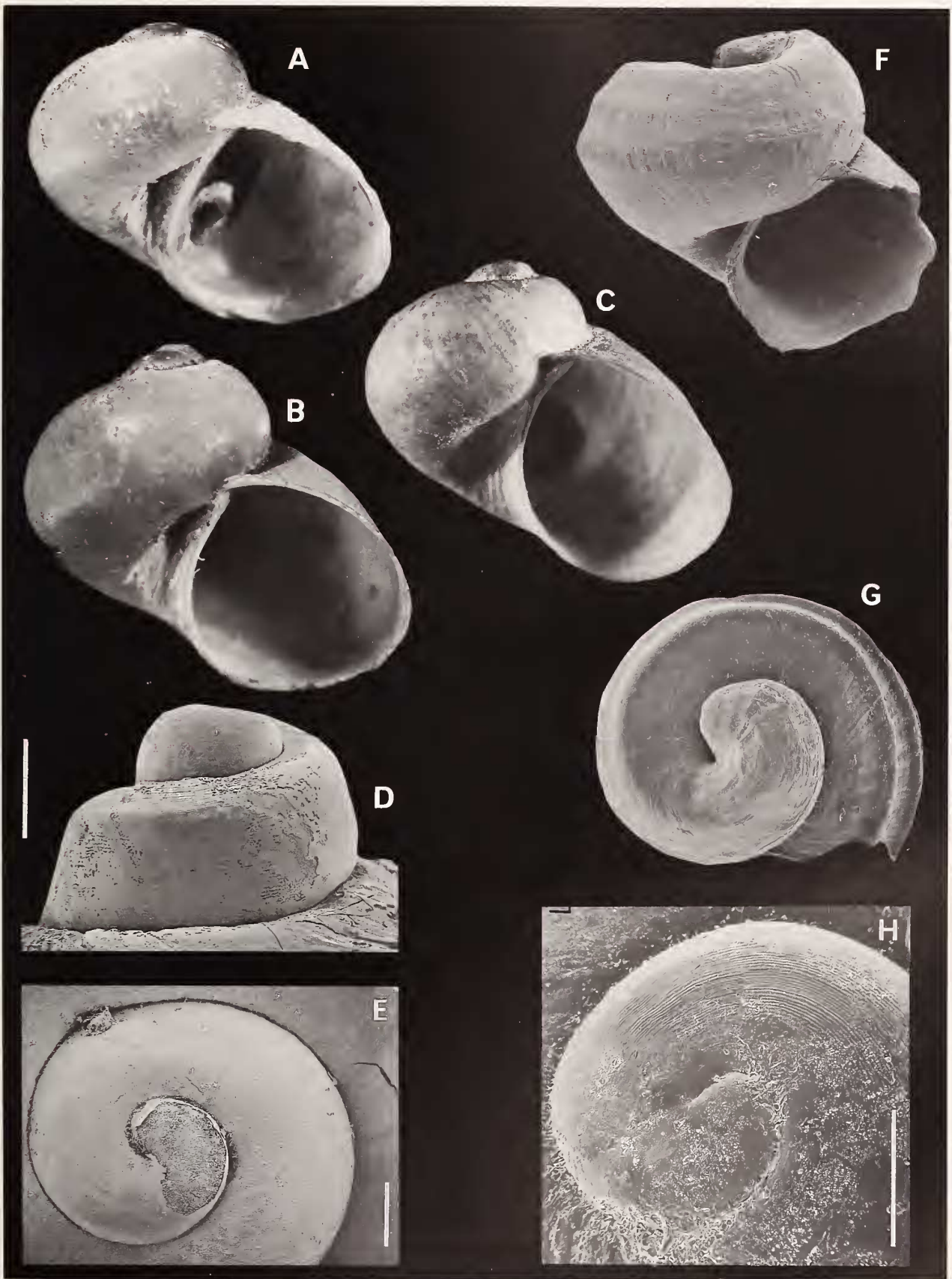
Two specimens were available for examination of the soft parts and radula. The radulae of two type specimens of *L. notorcadensis* were examined after rehydration and extraction of the soft parts. The soft parts of the type specimens were, however, too poorly preserved to allow examination of the external morphology.

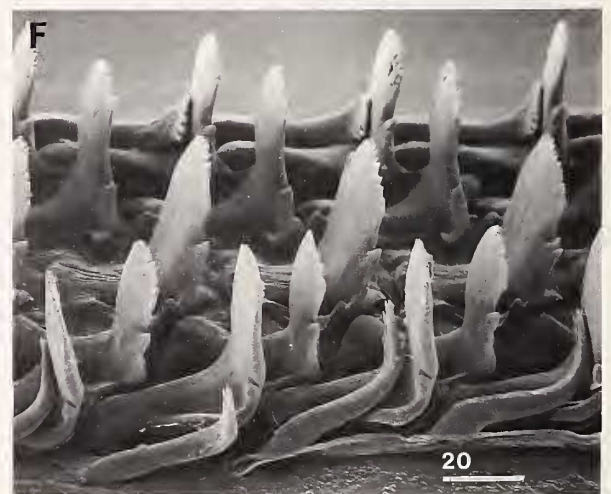
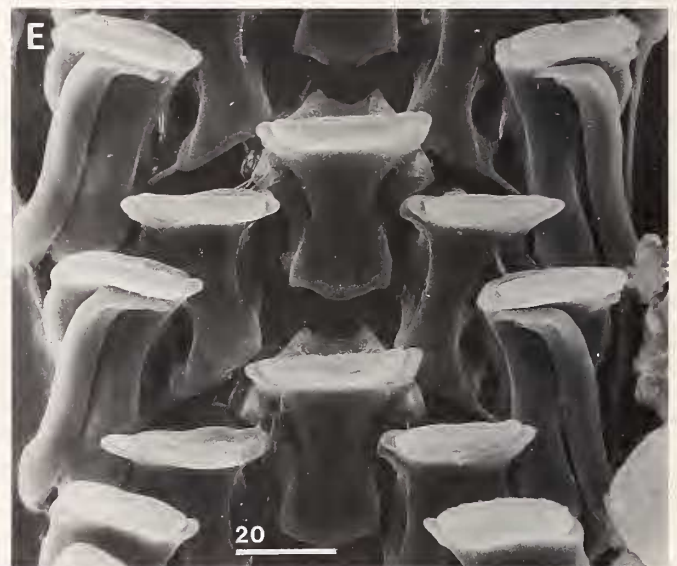
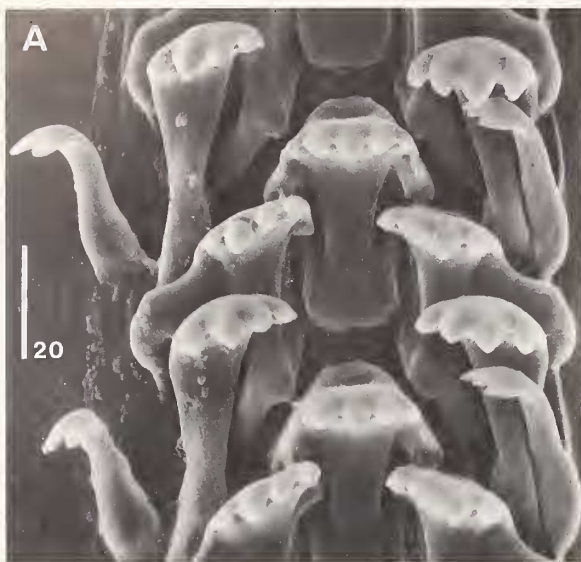
Lacuna wandelensis was referred to *Antitrichotropis* by Powell (1951:124, 1960:143). He may, however, have had a specimen of Trichotropidae, since he mentioned the presence of “odd tufts of hair-like processes disposed at regular intervals on the carinae.” Such are not present in *L. wandelensis*.

Dell (1990:162) suggested that *L. notorcadensis* may be a synonym of *Lacuna wandelensis*, an opinion we share.

Explanation of Figure 34

Figure A. *Haloconcha reflexa reflexa*, syntype, USNM 40928, diameter 3.7 mm. Figure B. *Haloconcha minor*, syntype, USNM 215073, diameter 6.3 mm. Figures C, H. *Laevitorina* (*Macquariella*) *antarctica*, South Georgia, Cumberland Bay, 1–2 m, on algae, SMNH 2794, diameter 4.7 mm. Figure D. *Laevitorina wandelensis* (paratype of *Lacuna notorcadensis*), apex, NMWZ 1955.158.157. Figure E. *Dickdellia labioflexa*, apex, PS VII/4, sta. 293. Figures F, G. *Trilirata macmurdensis*, PS IX/3, sta. 173, diameter 1.0 mm. Scale lines = 200 μ m.





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Explanation of Figure 35

Radulae, Littorinidae. Figure A. *Haloconcha reflexa*, syntype. Figure B. *Lacuna vincta*, Swedish west coast, Koster Area. Figures C, F. *Lacuna notorcadensis*, paratype, NMWZ 1955.158.157. Figure D. *Laevilitorina* (*Macquariella*) *antarctica*, South Georgia, Cumberland Bay, 1-2 m, on algae, SMNH 2794. Figure E. *Laevilitorina wandelensis* (holotype of *Lacuna notorcadensis*), RSM 1921.143.623. Scale lines in μm .

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